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THE SYSTEMATICS AND DISTRIBUTION OF *LOLIGO* (CEPHALOPODA, MYOPSIDA) IN THE WESTERN NORTH ATLANTIC, WITH DESCRIPTIONS OF TWO NEW SPECIES[1]

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ABSTRACT

The common squid *Loligo pealei* Lesueur, 1821, lives on the continental shelf and slope of the North and South American continents from Nova Scotia to the Gulf of Venezuela. Statistical analyses show that 1) females have a wider gladius and fewer gill filaments than males; there also is slight but statistically significant sexual dimorphism in 3 other characters; 2) populations vary but there are no clines in 50 anatomical measurements. However, southern *L. pealei* (Caribbean Sea-Gulf of Mexico) differ in the following ways from northern *L. pealei* (eastern United States Atlantic coast): 1) gill length increases faster in relation to mantle length in the southern squid; 2) there is more variation in the hectocotylus and number of buccal lappets in the southern squid.

Variation in *Loligo pealei* appears greater in areas of sympatry with *L. plei* (= *Doryteuthis plei*); much of this variation takes the form of greater resemblance to *L. plei*. These 2 species overlap in almost all characters. The ratio of the greatest width of the gladius vane to the greatest width of the free rachis can be used to distinguish the 2 species. The geographic range of each species is redefined.

Two new species of *Loligo* are described: *Loligo ocula*, a large-eyed species caught at 256-362 m in the Caribbean Sea and between Cuba and the Bahamas, and *Loligo roperi*, a small species from the Caribbean.

The 4 species are compared. In many characters they show the following relationships: *Loligo ocula* is most similar to *L. pealei*; *L. pealei* is also similar to *L. plei*; *L. plei* is most similar to *L. pealei*, but is also similar to *L. roperi*; *L. roperi* is the most distinctive of the 4 species.

Loligo roperi matures at a small size and then apparently ceases growing or does not survive spawning; it may be a somewhat neotenic relative of *L. plei*. The larger eyes in *L. ocula* (and correspondingly larger head and mantle width) may be an adaptation to living at depths greater than are typical for the Loliginidae.

In the western North Atlantic, the greatest species diversity for both *Loligo* and the Loliginidae occurs in the Caribbean Sea. A key to these 4 species of *Loligo* of the western North Atlantic Ocean is given.

INTRODUCTION

Interest in *Loligo pealei* Lesueur, 1821, as a fisheries resource for bait and food, and as a source of large axons for neurological research, has stimulated many studies—chiefly of populations that occur between Cape Hatteras and Nova Scotia.

The purpose of this study is to clarify the systematic status of a taxonomically confused group of commercially important cephalopods. Considerable variation has been noted in *Loligo pealei*; some specimens of *L. pealei* are so similar to some specimens of *L. plei* Blainville, 1823, that misidentifications often occur in spite of existing keys (Voss, 1956: 91). Verrill (1880, 1881), Arnold (1962), LaRoe (1967), and Voss (personal communication) have suggested that variation in *L. pealei* is geographic. This study examines variation in *L. pealei* and describes and compares the 3 other species of *Loligo* which are partially sympatric with *L. pealei.*

Loligo pealei is the most widely distributed of the neritic squid in the western Atlantic (LaRoe, 1967), where it has been reported to extend from Nova Scotia (Mercer, 1970a) to Colombia (LaRoe, 1967). This is a latitudinal distance of more than 35 degrees and includes the Caribbean Sea, the Gulf of Mexico, and the Atlantic coast of North America (Fig. 1).

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[1] Part of this investigation was done in partial fulfillment of the requirements for the degree of Master of Science, University of Maryland.

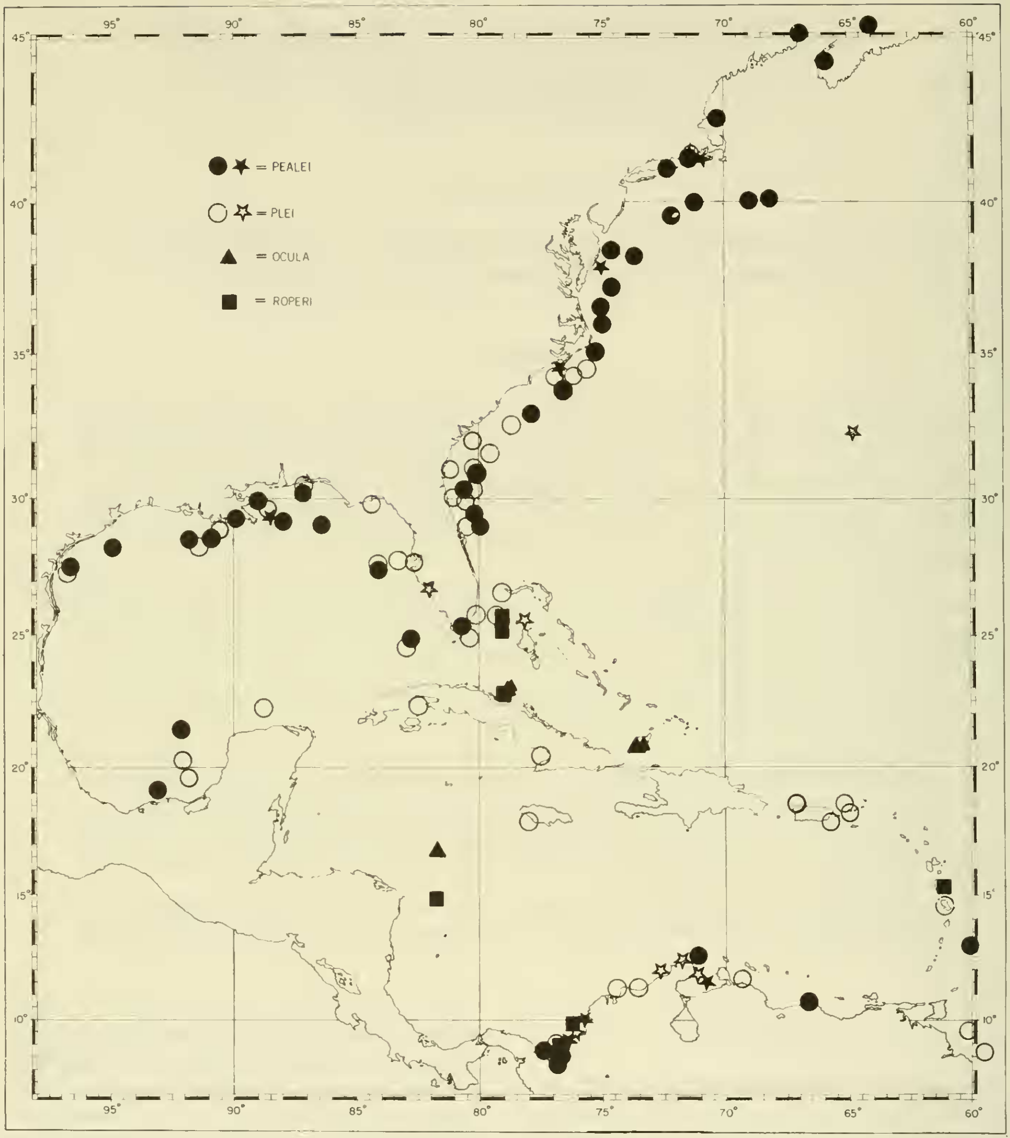


FIG. 1. Map showing location of statistical samples of *Loligo pealei* and *L. plei* and other records of capture of *L. pealei, L. plei, L. ocula,* and *L. roperi.*

MATERIALS AND METHODS

MATERIALS: All material studied is listed in the species descriptions or in Appendix A. Most of the material for this study was provided by the Smithsonian Institution. Material was also provided by the Marine Biological Laboratory of Woods Hole, the Rosenstiel School of Marine and Atmospheric Sciences at the University of Miami, the Florida State Board of Conservation, the National Marine Fisheries Service, and J. Ewald of the Fisheries Research and Development Project, Food and Agricultural Organization of the United Nations.

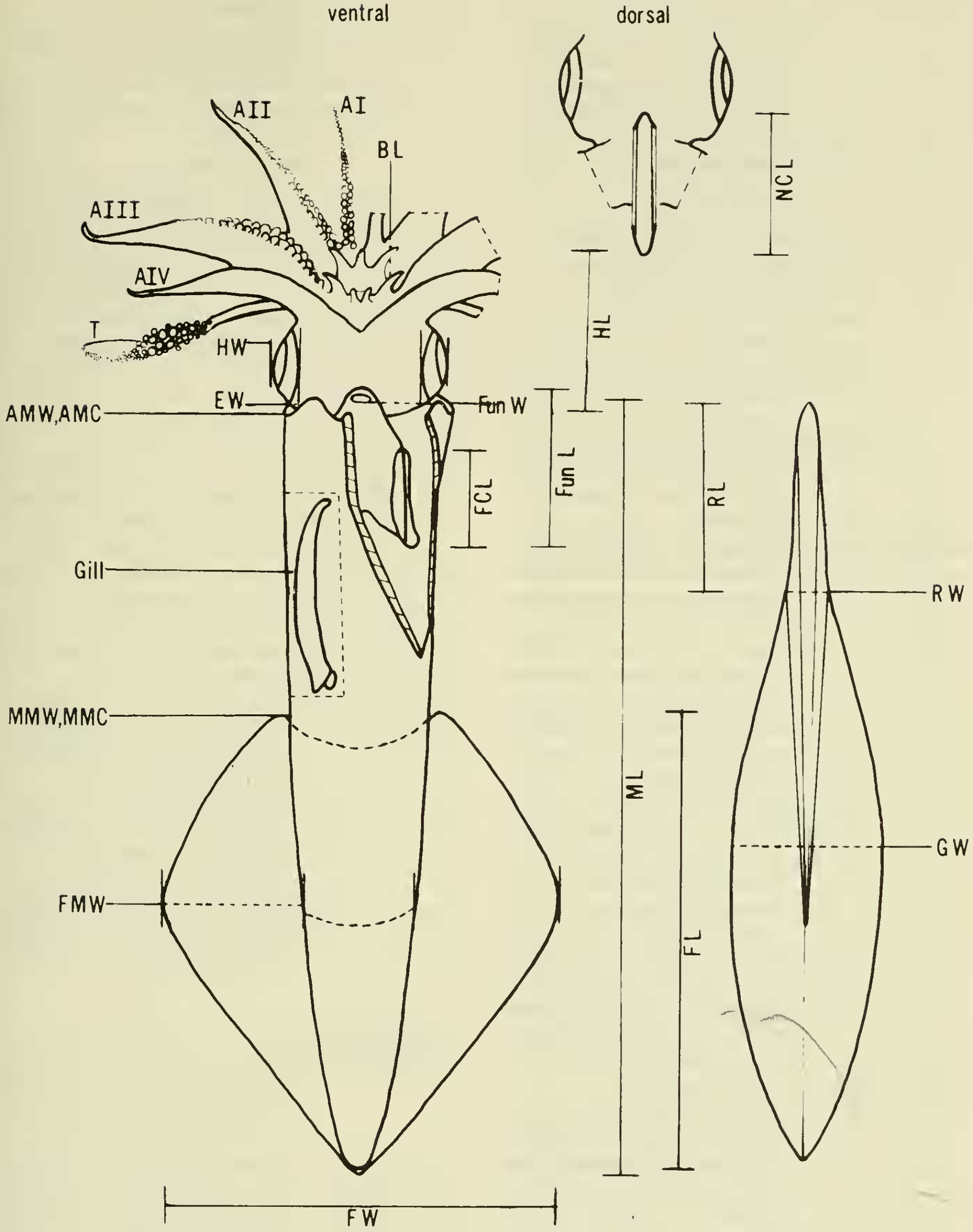


FIG. 2. Diagram of measurements.

DESCRIPTION OF MEASUREMENTS: Most of the measurements in the following list are shown in Fig. 2. Dorsal, ventral, anterior and posterior refer to orientation of the adult in life.

MEASUREMENTS:

AL	arm lengths measured from proximal-most sucker to arm tip on right arms. (Left arm measured if a right one was missing. Only right ventral arm of males used because left ventral male arm is hectocotylized.)
ALI	length of 1st or dorsal arm.
ALII	length of 2nd arm.
ALIII	length of 3rd arm.
ALIV	length of 4th or ventral arm.
AMC	mantle circumference measured at anterior border (opening).
AMW	mantle width at anterior border (opening) with mantle held as cylindrical as possible.
ASW I, II, III, IV	greatest width of largest sucker on right (left if right arm is missing) arms I-IV.
BE	distance between median borders of eyes with head compressed.
ED	greatest diameter of white eyeball visible externally through cornea.
FCL	greatest length of entire right funnel cartilage.
FL	fin length from point on dorsal mantle midway between fin insertion, to posterior body tip.
FMW	mantle width coincident with widest point of fins.
Fun L	ventral funnel length from midpoint of anterior opening to midpoint of posterior border.
Fun W	greatest width of anterior funnel opening measured by spreading dividers as widely as possible inside orifice.
FW	greatest width of both fins between lateral-most points.
Gill F	number of outside filaments on right gill.
Gill L	length of right gill from proximal attachment of branchial vein to gill tip.
Gill W	greatest width of right gill.
GW	greatest width of vane of gladius.
HAL	length of hectocotylized arm.
HCL	length of hectocotylus from its origin proximally to arm tip.
HL	head length from anterior tip of nuchal crest to juncture of dorsal arms.
HW	greatest head width at level of eyes with head strongly ventro-dorsally compressed between two fingers.
LD	diameter of dissected lens.
ML	length of mantle from anterior tip of mid-dorsal point to posterior body tip.
MMC	mid-mantle circumference at level of fin insertion.
MMW	mid-mantle width at level of fin insertion.
NCL	greatest length of entire nuchal cartilage.
RL	length of free rachis.
RW	greatest width of rachis of gladius.
TCL	length of right tentacular club (left if right club is missing) from proximal-most sucker to tip.
TL	length of right (left if right tentacle is missing) tentacle from origin between A III and IV to tip.
TSW	greatest width of largest sucker on right (left if right tentacle is missing) tentacle.

COUNTS:

ASI, II, III, IV	total number of suckers on right arms I, II, III, IV (left arm used if part of right arm missing).
BLS 1,2,3,4-5,6,7	number of suckers on each buccal lappet (counting counter-clockwise beginning with mid-dorsal lappet).
H	number of modified suckers on hectocotylus in the dorsal row that are less than 1/2 the size of their partners in the ventral row.
HAS	total number of suckers

on hectocotylized arm from proximal-most modified sucker to arm tip.

TSR number of transverse rows of suckers across right (left if right tentacle is missing) tentacular club (4 suckers in each row).

For convenience, males were considered mature if spermatophores were present in Needham's sac, and females were counted as mature if the ovaries were filled with eggs; since this method is inadequate in recently spent animals, the lengths of penises and female accessory nidamental glands were recorded.

Most measurements were made with dividers and a ruler with 0.5 mm divisions, and were recorded to the nearest mm. Sucker widths were measured with a micrometer caliper with 0.05 mm divisions and recorded to the nearest 0.1 mm.

AMC and MMC were measured with a steel tape with 1 mm divisions. Because the mantle wall is often very flaccid, circumference probably is a more accurate measurement than width. Both measurements were made because MW is widely used by others.

Arm tips and gills were stained with methyl blue solution to facilitate counting of suckers and gill filaments. The largest suckers were removed from the right 3rd arms and the tentacles of 52 specimens of *Loligo pealei* and 10 specimens of *L. plei* and glued to cardboard slides with a numbered grid for comparison of dentition. Spermatophores were mounted on glass slides with Turtox CMC-10 mounting medium; after several months they deteriorated.

Gladius length was not measured because of the difficulty in removing the entire gladius intact from many specimens and because gladius length is almost the same as ML which is measured directly over the gladius.

Other measurements taken initially but discontinued include the number of muscle strands in the fin (too difficult to count) and the number of suckers from the base of the arm to a point on the arm equal to 1/5 ML (results influenced by AL:ML). The following measurements were discontinued because the results did not show any useful pattern: the number of suckers on the basal half of the arm, the angle of the vane of the gladius at its origin on the rachis, distance between the insertion of the fins, and dimensions of the funnel valve.

STATISTICAL ANALYSES: Data were analyzed on the UNIVAC 1108 at the Computer Science Center of the University of Maryland with canned computer programs. The BMDO2D and BMDO3D (Dixon, 1970) were used to obtain means, standard deviations, correlation coefficients, sums of squares and cross plots.

Many characters of *Loligo pealei* change with growth. Haefner (1964) found that indices (dividing by ML) of FW, FL, MW, HL, and HW change with growth in *L. pealei*. Since it was impossible to get samples of equal size for comparison, an analysis of these characters that would eliminate the effect of differences due to growth was made. Covariance (ANCOVA) analyses were done with the Manova program (Biometric Laboratory, no date). This program allowed the analysis of the factors of geographic location and sex simultaneously and printed out means, standard deviations, variance and covariance tables, F values, probabilities for F values for regressions and factors, grand means, deviations of factor means from grand means, and within regression coefficients and intercepts.

When a significant F value was found, a Studentized Range Q test (Snedecor & Cochran, 1969: 272-274) was used to find significant differences between factor means. Differences between 2 regressions were tested by the method of Snedecor & Cochran (1969: 432-435).

Analyses were made using ML and FCL as independent variable and covariate. ML is the commonly used measure of standard length in squid. FCL was used because FCL shows higher correlations with many characters than ML does (Tables 4 and 5), because fewer inequalities of variance occur with FCL than with ML, and because of the results of the preservation experiment (discussed below). In those cases in which similar results were obtained with analysis using ML and FCL, ML is the independent variable shown in graphs illustrating this study because ML is the common measure of standard length. Statistical results (analysis of covariance and regression equations) are given in Appendix B.

EFFECTS OF PRESERVATION

Preservation with formalin has been found to shorten the length of fishes. For example, *Oncorhynchus* shrank 3% after 12 hours in 3.8% formalin and 1% more after 30-40 days; further changes in length were insignificant (Parker, 1963). *Oncorhynchus* shrank 4.6-6.8% after 5.5 months in 10% formalin; about 80% of the total decrease occurred in the first 24 hours.

In the squid *Loligo pealei* and *Lolliguncula brevis*, Haefner (1964) reported more than 5% shrinkage in the length of arms and tentacles after preservation in 5% formalin.

Methods of preservation of most samples available for this study were suspected to be different; this could cause artificial differences in measured characters. I was able to collect only 2 fresh samples; one, consisting of 44 specimens, was divided into 3 parts and preserved by 3 different methods. Covariance analyses were made to determine if differences in techniques of preservation caused significant differences in any measurements. The methods of preservation were: 1) 9 specimens (86-188 mm ML) were kept on ice and refrigerated for 2 days before being preserved in 10% formalin. After 16 days they were rinsed and placed in 40% isopropyl alcohol. 2) 22 specimens (76-244 mm ML) were preserved in 10% formalin immediately after capture, then rinsed and placed in isopropyl alcohol 2 days later. 3) 13 specimens (130-234 mm ML) were preserved in 10% formalin immediately after capture, then rinsed and placed in isopropyl alcohol 16 days later.

Results of this experiment are shown in Table 1. When formalin preservation is delayed (method 1), the size of AL II and TL are statistically significantly larger when either ML or FCL are used as covariates.

FCL is also statistically significantly greater under method 1 with ML as covariate. The following results are probably related to the relationship between ML and FCL. Statistically significant difference in these variables depends on which of the 2 covariates is used with them. When ML is used as covariate (but not when FCL is used as covariate) the following measurements are statistically significantly higher in method 1, when formalin preservation is delayed, than in methods 2 and 3: HL, ALI, ALIII, ALIV, TCL, ASW III, Fun L, and Fun W. Sucker widths of the other arms were not tested but it is likely that they would show similar results.

When FCL is used as covariate (but not when ML is used as covariate) the following measurements are statistically significantly smaller when formalin preservation is delayed: FL, FW, MMW, and NCL. In order to eliminate bias between specimens which have been preserved differently, it is necessary to use the covariate (ML or FCL) with which the measurement has shown no preservation differences.

TABLE 1. Measurements of *Loligo pealei* significantly affected by differences in the method of preservation ($p < 0.05$).

Measurement	Covariate*	Significant difference between adjusted means in mm		Sample size		
		Method 1 minus Method 2	Method 1 minus Method 3	Method 1	Method 2	Method 3
ALII	ML	12.1	8.6	9	16	10
ALII	FCL	6.8	–	9	16	–
TL	ML	49.3	39.7	8	21	12
TL	FCL	39.5	29.4	8	21	12
FCL	ML	2.0	–	9	16	–
HL	ML	6.0	–	9	16	–
ALI	ML	10.2	6.6	9	16	10
ALIII	ML	11.0	9.6	9	16	10
ALIV	ML	8.8	7.3	9	16	10
TCL	ML	8.7	7.2	8	21	12
ASWIII	ML	0.32	–	9	16	–
Fun L	ML	2.6	–	9	16	–
Fun W	ML	1.7	–	9	16	–
FL	FCL	–16.9	–16.2	9	16	10
FW	FCL	–10.2	–	9	16	–
MMW	FCL	–2.2	–3.5	9	16	10
NCL	FCL	–2.3	–	9	16	–

*Covariance was effective in all cases. P less than 0.001 for F test of mean square due to regression.

HW, AMW, MMC, Gill L, and GW show no significant preservation differences using either ML or FCL as covariates. There are no significant differences between methods 2 and 3 for any measurements.

Differences in preservation did not affect tests for sexual dimorphism since both sexes were present in all samples. Effects of preservation would have to be considered in comparing geographically different population samples since these were preserved differently by different collectors. Past descriptions of *Loligo pealei* and probably other species of squid may be biased in the measurements which are affected by preservation differences.

A more comprehensive experiment to determine the full extent of preservation differences would be worthwhile. A larger sample should be tested. Delays in fixation of 1 week or even 2 weeks should be tested as preservation is sometimes delayed that long when squid are iced or frozen on board ship and not preserved in formalin until port is reached.

This experiment did not show 1) whether both covariates, FCL and ML, shrink less when preservation is delayed but FCL shrinks even less than ML, or 2) whether both shrink more when preservation is delayed, but ML shrinks even more than FCL. An experiment including measurements of fresh specimens would be necessary to determine this. FCL is a measurement made directly upon a rigid structure and it is unlikely that it shrinks much with preservation. ML is a fairly reliable measurement because it is made where the mantle overlies and is rigidly supported by the attached rigid chitinous gladius. ML was measured on 7 specimens before and after immediate fixation; preservation caused as much as 6% shrinkage. LaRoe (1967) found shrinkage in 15 immediately preserved specimens averaged 1.2% with a maximum of less than 2.5%. The entire gladius was removed from some specimens and it is often a few mm shorter than the ML measured before removal. Such removal of the supporting gladius shortens the mantle.

The Smithsonian Institution has many specimens collected by A. E. Verrill between 1875 and 1880. Verrill, in his publications, listed many of the measurements of these specimens along with remarks on their preservation (Verrill, 1881). I found 6 of these specimens with Verrill's identifying numbers still tied to them and in 1972 remeasured them twice. The specimens were originally 124-254 mm ML and bear Verrill's numbers: DD♀, HH♀, IV♀, 8V♂, d♂, and c♂. Table 2 shows the results. These specimens had been stored in 70% ethanol for 92-97 years between the time of Verrill's measurements and mine. The sample is very small. I cannot know how my methods of measurements differed from Verrill's; however there was sometimes a greater difference between my 2 measurements than between mine and Verrill's. Mantle length shrank slightly. Fin width was shorter or the same in 5 specimens and slightly wider in one. Head width and tentacular club length were greater. Mantle width and circumference were less in 4 specimens and greater in 2. Change in the other measurements was more inconsistent.

The small change in mantle length agrees with Parker's (1963) and Burgner's (1962) report that in the fish *Oncorhynchus* most shrinkage in length occurs only in the first day after preservation. While delay in preservation affects some measurements of squid, well-kept museum specimens may not change greatly in morphometrics following the changes which occur at death and initial preservation.

TABLE 2. Morphometric changes in *Loligo pealei* after 92 years of storage in 70% ethyl alcohol.

Measurement	n	Average difference between Verrill and Cohen measurements, mm	Effect	Average change %	Greatest single change %
Mantle length	6	−1.9	shorter	1.0	1.6
Fin length	6	−1.7	inconsistent	2.8	12.0
Fin width	6	−3.3	shorter	3.6	6.8
Head width	5	+3.0	wider	9.9	19.0
Mantle width	6	−1.4	inconsistent	12.0	13.0
Mantle circumference	6	−3.4	inconsistent	5.5	13.0
Tentacular club length	5	+1.6	longer	7.9	20.0
Tentacular sucker width	3	0.0	inconsistent	0.0	9.1
Arm III sucker width	3	−0.17	inconsistent	6.4	20.0

SYSTEMATICS

Loligo pealei Lesueur, 1821
(Figs. 3-4)

Loligo pealeii Lesueur, 1821: 92-94, pl. 8.—Férussac & d'Orbigny, 1834-48, pl. 11.—Drew, 1911: 327-359; 1919: 379-418.

Loligo pealei Lesueur.—Férussac & d'Orbigny, 1834-48: 311-312.—Verrill, 1880: 292-293; 1881: 308-343, pl. 29, figs. 1-4, pl. 37, figs. 1-3, pl. 39, fig. 4, pl. 40, pl. 41, pl. 45, figs. 3-4.—Voss, 1956: 112-115, fig. 5; 1962: 1; 1973: 24-25.—Dillon & Dial, 1962: 156-166.—Summers, 1968: 366-367; 1969: 202-216; 1971: 189-201.—Summers & McMahon, 1970: 389-396.

Loligo pallida Verrill, 1873: 635-636, pl. 20, figs. 101, 101a; 1874: 169-170, figs. 54-55; 1880: 293.

Loligo pealei Lesueur var. *borealis* Verrill, 1880: 284-295; 1881: 308, 316-317, pl. 37, fig. 2, pl. 41, fig. 1.

Loligo pealei Lesueur var. *pallida* Verrill.—Verrill, 1881: 308, 317-318, pl. 34, figs. 1-4, pl. 37, figs. 9-11, pl. 40, fig. 1.

Loligo pealii Lesueur.—Verrill, 1874: 170-172.—Williams, 1909: 1-92.—Stevenson, 1934: 4-7, figs. 1-2.—Adam, 1937: 62-63, fig. 16.—Arnold, 1962: 53-57.

DIAGNOSIS: Ratio of greatest width of vane of gladius to greatest width of free rachis 2.4-2.9 in males, 2.7-3.7 in females; hectocotylus originating in distal 1/3-1/4 of left ventral arm, not extending to arm tip, not more than about 12 suckers in dorsal row less than 1/2 the size of their ventral counterparts, at least some modified suckers of dorsal row with narrow bases.

DESCRIPTION: *Mantle* long, moderately slender, cylindrical, tapering to a posterior rounded point. Anterior mantle width 14-37% of ML (25-315 mm ML); anterior mantle circumference 39-44% of ML (95-244 mm ML); longer specimens more slender. Ventrolateral lobes on mantle opening short and pointed (point approximately 90° angle, usually slightly acute, sometimes slightly rounded); dorsal lobe larger than lateral lobes, with rounded point. Low, narrow mid-ventral ridge present (mostly in males).

Fins rhomboid, sides fairly straight, widest point curved and slightly anterior of midpoint of fin length; fins united posterior to tip of mantle; width about 34-56% of ML (45-315 mm ML); length about 44-64% of ML (45-314 mm ML); width about equal to length; ratio of length to width = 0.812-1.88 (64-315 mm ML). Fins relatively longer and more narrow in longer specimens; anterior lobes well-developed.

Funnel well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheet-like. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute and rounded or pointed at tip. Ventral pads oblong, shorter than dorsal organ. Funnel valve broad, blunt or bluntly rounded, with thin curved lateral flaps.

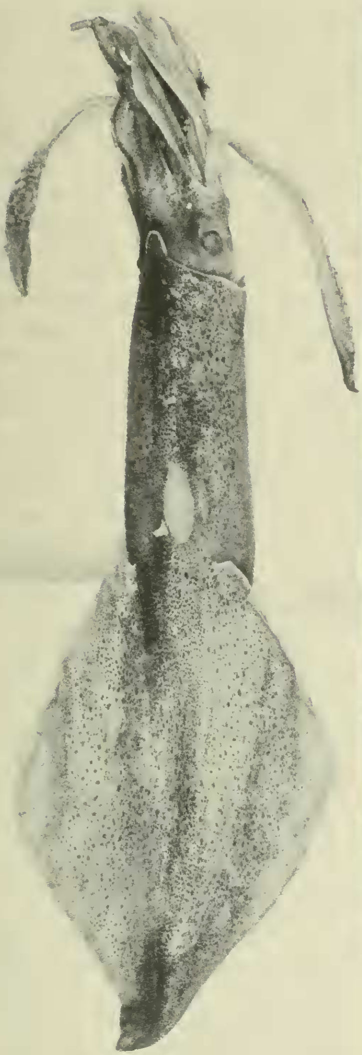
Funnel locking-cartilage long (about 10-18% of ML, 60-314 mm ML), straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head width about 12-33% of ML (45-314 mm ML); length about 10-30% of ML (70-315 mm ML); head relatively smaller in longer specimens; nuchal cartilage long, about 13-22% of ML (60-273 mm ML), cartilage relatively shorter in longer specimens, straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to blunt or rounded points; shallow central groove, lateral ridges distinct.

Eyes oval, covered by cornea, pupil round. Diameter of externally visible eyeball about 8-18% of ML (25-237 mm ML). Diameter of dissected lens about 2-6% of ML (72-291 mm ML). Dark, rarely greenish, crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order usually III>II>IV>I or III>IV≥II>I, occasionally III>II>I>IV, III>IV>I>II, III>I>II>IV, II>III>I>IV, II>IV>III>I, IV>III>II>I, IV>II>III>I. Length of arm I about 19-50% of ML; length of arm II about 22-50% of ML; length of arm III about 26-45% of ML; length of arm

FIG. 3. Examples of *Loligo pealei* showing variation in relative proportions of mantle and fin; **a**, ♂, 214 mm ML; *Cynthia*, Cohen statistical sample no. 20; **b**, ♀, 179 mm ML; Cohen spec. no. 8, stat. sample no. 1; **c**, ♂, 70 mm ML; York Spit Light, Chesapeake Bay, 2 July 1968.



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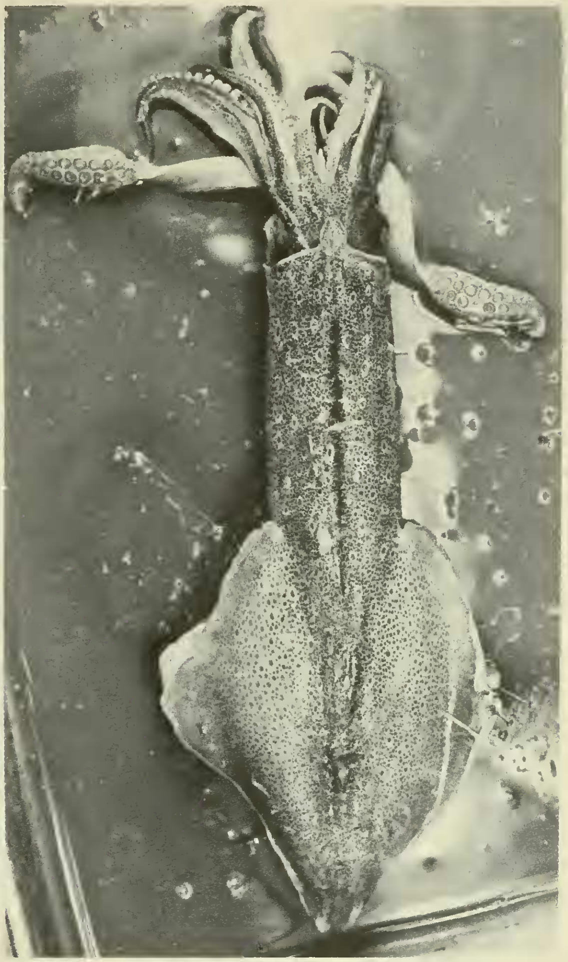

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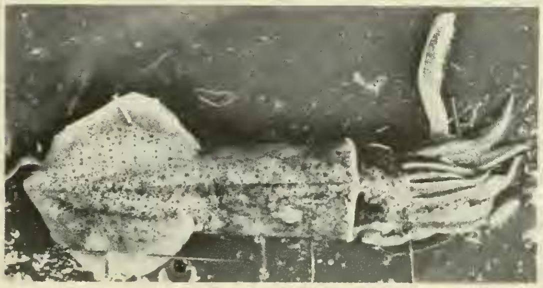

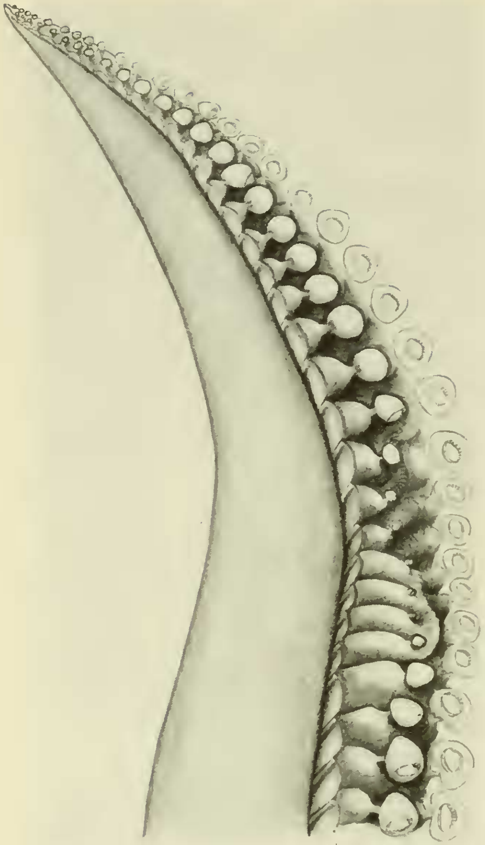

FIG. 4. *Loligo pealei* hectocotylus; 244 mm ML; *Cynthia,* Cohen spec. no. 272, statistical sample no. 13; distal 20 mm (distal third) of arm shown.

IV about 22-38% of ML (60-315 mm ML). Arm III robust, IV, II less robust, I least robust, very slender. Swimming keels third-best developed on arm I, flaring before midpoint, decreased to very low distally; very low, weak on arm II, decreased distally; best-developed on arm III, flared before midpoint, decreased gradually distally; second-best developed on arm IV, 2 keels decreased gradually distally, dorsal keel better-developed, dorsal keel of arm IV and keel of arm III arising from same area at base of arms. Protective membranes well-developed, particularly ventral membranes on arms I, II, III; poorly developed, particularly dorsal membrane, on arm IV; trabeculae long, strong, except on arm IV, arise from base of sucker stalks, form high points along membranes. Suckers biserial. Distad increase in size of about 5-10 proximal-most suckers on arms I, II, III, sometimes IV; gradual decrease in size of succeeding suckers; rapid decrease in size of suckers on arm III following about 20th-25th sucker. Number of suckers on arms increases with mantle length; number of suckers on arms I, II, III about equal, about 10 more suckers on arm IV than on other arms; about 65-125 suckers on arm I, about 70-125 suckers on arms II, III, about 84-132 suckers on arm IV (40-315 mm ML). Width of suckers on arms in order III⩾II⩾I⩾IV.

Arm sucker dentition variable. Teeth usually present on distal 1/2 of tooth ring only. Proximal 1/2 of tooth ring usually low, broad plate, occasionally rippled, rarely defined into about 10-20 tiny blunt teeth. About 6-10 teeth on distal 1/2 of arm I; about 7-12 teeth on distal 1/2 of arm II; about 6-11 teeth on distal 1/2 of arm III; about 5-8 teeth on distal 1/2 of arm IV. Teeth shape and pattern varies, tips of teeth usually blunt or rounded, apparently never pointed; teeth sometimes square, center 1-4 teeth often narrowest, teeth decrease in size laterally, pattern not always symmetrical.

Left ventral arm *hectocotylized* (Fig. 4), modification in distal 1/3 to 1/4 of arm, chiefly in dorsal sucker row, does not extend to tip of arm; usually only 10-12 suckers in the dorsal row less than 1/2 the size of their ventral counterparts (range of variation observed 5-17). About 34-61 suckers proximal to hectocotylus, proximal-most about 6-24 suckers increasing slightly in size distally, followed by suckers of slightly decreasing size. About 52-82 suckers distal to origin of hectocotylus; hectocotylization originates proximally with about 2-5 suckers in the dorsal row diminishing in sucker size and increasing in pedicel height, followed by 1-4 tiny suckers on long pedicels, followed by 2-5 tiny suckers on pedicels of decreasing height, followed by 5-8 suckers of increasing size; ventral suckers in modified area reduced slightly, at least twice the size of their dorsal counterparts, pedicels normal; suckers distal to modified area normal in both rows except dorsal suckers often slightly smaller than ventral suckers. Central area of arm in modified area raised, puffy and folded with central ridge connecting the folded bases of the arms.

Tentacles robust. Clubs expanded, about 20 to 38% of ML (60-315 mm ML). Clubs with 30-45 transverse rows of 4 suckers each (20-315 mm ML). Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 1-3 suckers; no carpal knobs. Often only 3 small suckers in proximal-most row of manal suckers; distal rows tetraserial; suckers gradually increase in size; lateral manal suckers smaller than medial suckers; about 12-17 medial suckers on manus greatly enlarged; manus terminates rather abruptly; distal-most 1 or 2 transverse rows of manal suckers decrease in size, lateral suckers more equal in size to medial suckers, ventral lateral sucker becomes larger than dorsal lateral sucker of same transverse row and this size difference sometimes continues for as many as 14 rows of the dactylus. Dactylus distinct, slender, suckers tetraserial, numerous, minute, decreasing in size distally; distal-most 2 transverse rows often triserial and biserial. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of stalk aborally, increases in size on club particularly on distal 1/3 of manus, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad, heavily supported protective membranes along club, diminish significantly along dactylus; dorsal membrane slightly smaller than ventral membrane along manus and insignificant along dactylus. Broad trabeculae between lateral suckers, usually broaden laterally as a fan shape, arise from common base of lateral suckers, particularly the distal sucker; contribution from proximal sucker also in many larger specimens. Width of largest tentacular sucker almost always larger than width of largest sucker on arm III; ratio of width of largest sucker of tentacle to width of largest sucker on arm III: 0.72-2.1.

Club sucker dentition variable. About 8-30 teeth, usually about 20, on sucker rings of carpal area, varying from blunt to pointed, graded in size; teeth on 1/2 of ring very small, sometimes only a rippled edge, about 4-13 large teeth. About 20-35 teeth on largest lateral manal suckers; teeth usually pointed, graded in size, sometimes alternating large and small teeth; teeth at outer edge of ring larger and usually more pointed than inner teeth. About 35-65 teeth on largest medial manal suckers; teeth usually pointed, usually triangular in shape, points sometimes slightly curved; patterns of teeth arrangement vary, teeth often arranged in a pattern of alternating large and small teeth, many specimens have at least some teeth arranged in a trinary pattern in the following sequence: large tooth, small tooth, medium tooth, small tooth, large tooth; occasionally teeth are of almost equal size. Proximal dactylar sucker rings with about 16-22 pointed teeth, graded in size; about 6-10 larger teeth.

Gladius long, rather wide (about 10-20% of ML, 23-224 mm ML), feather-shaped; anterior tip with weak flexible acute point; rachis stiff, free rachis length about 7-33% of ML (23-224 mm ML); median ridge and strong lateral rods on rachis, continue in center of vane, fuse beyond midpoint of vane, extend length of gladius. Additional lateral colored bands often occur near edge of vane; these bands rarely thickened into a weak to strong lateral rod in males; lateral edges of vane usually thin and weak. Sides of vane usually curved (fairly straight in some males); vane usually tapers at both ends, widest point in central area. Rachis rather narrow, gladius rather wide; ratio of greatest width of vane to greatest width of rachis about 2.4-3.2 (2.1 in one specimen).

Buccal lappets usually 7 (rarely 6, 8, 9); 7 buccal connectives, 7 supporting rods, suckers present on each lappet (maximum of 19); total suckers on all lappets about 35-113 (44-315 mm ML). Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I-IV respectively.

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella); weak, thin, lightly pigmented, notch separates rostrum and rostral lamella (jaw angle recessed); cutting edge of rostral lamella straight; palatine lamella weak, large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge curved, jaw angle obtuse but nearly 90°; rostral lamellae narrow, short, wing lobate, thin; gular lamella large, crest strong, posterior corner pointed, moderately curved.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth, pointed lateral cusps; 1st lateral tooth pointed with pointed lateral cusp; 2nd lateral tooth pointed, longer than first, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 74-79% of total length, cement body about

7-9% of total length (153-291 mm ML), total length about 4-13 mm (70-291 mm ML). Oral connection of cement body cylindrical, narrows at oral end.

Gill length about 23-34% of ML (55-315 mm ML). Number of filaments on 1 side of gill increases with ML.

Color (in alcohol). Reddish-brown chromatophores present on entire mantle, larger and more closely-spaced on dorsal side, particularly in mid-dorsal region; present only on dorsal side of fins; cover entire head, more closely-spaced dorsally, particularly proximal to eyes; present on collar and funnel, on outer sides of arms, tentacles, trabeculae and protective membranes of arms I, II, III, tentacles. Dark crescent over dorsal borders of eyes. Reddish-brown anterior mid-dorsal longitudinal indentation.

HOLOTYPE: Deposited at the Academy of Natural Sciences of Philadelphia, but missing (Voss, 1962).

TYPE LOCALITY: South Carolina?

DISTRIBUTION: Continental shelf and slope of the E coast of the North and the N coast of the South American continents from Nova Scotia to the Gulf of Venezuela; very rare occurrences off islands near continents in the Bahamas and Caribbean. See Fig. 1. Dip-netted at the surface and taken in bottom trawls down to 393 m.

DISCUSSION:

Nomenclature: Loligo pealei was described by Lesueur (1821), who named it after R. Peale, manager of the Philadelphia Museum and source of the original specimens. Mr. R. Peale probably was the naturalist, Rubens Peale, son of Charles Wilson Peale, painter of portraits of George Washington (Malone, 1934).

The original spelling is *Loligo pealeii*, which is the correct spelling according to Article 32 of the *International Code of Zoological Nomenclature* (1964: 32-33), although according to Article 31A, the recommended ending for a patronymic specific name is a single *"i"*. The commonly used spelling for this species is now *L. pealei*. The International Commission on Zoological Nomenclature is now considering a request (Smith, Stuart & Conant, 1971: 250-252) to revise Article 32 to permit or require usage of the single *"i"* ending for a species-group name regardless of its original spelling. Smith et al. pointed out that the single *"i"* was required by the 1961 Code, is in better conformance with the rules of classical Latin, and is increasingly popular among taxonomists. I prefer the single *"i"* ending and will use it pending a decision by the Commission. The species name has also been spelled *L. pealii* (Ghiretti, 1966: 202; Williams, 1909) and *L. peali* (Brown, 1956: 153).

Loligo pealei commonly is known as the long-finned, common or winter squid (Lyles, 1968).

Geographic distribution: Loligo pealei is found as far N as Nova Scotia, Canada. The most northern specimen which I have identified is a juvenile (10.6 mm ML) collected in Minas Basin, Nova Scotia (USNM collection). Stevenson (1934) observed spawning schools of *L. pealei* in New Brunswick, Canada. The most southeastern *L. pealei* which I have identified are 10 mature specimens from the Gulf of Venezuela, Venezuela. Only 4 Loliginidae from Guiana, 6 from Mar del Plata, Brazil, and 4 from Rio Grande do Sul, Brazil, were available to me. They are not *L. pealei* and there are no reports of *L. pealei* from that far S. Francisco Palacio, University of Miami (personal communication) found no *L. pealei* in a collection of squid from Brazil; the bulk of his material came from the area between Rio de Janeiro and São Paulo. The 4 specimens from Guiana are probably *Loligo surinamensis* Voss (1974).

Voss (1973) states that the range of *Loligo pealei* is the continental shelf from Cape Cod S to Florida and the Gulf of Mexico, and possibly into the Caribbean Sea. On a map showing the distribution of *L. pealei*, Voss (1971: 309-310) showed *L. pealei* distributed along the E coast of the United States as far N as New York and present along the shores of the islands of the Caribbean Sea, the Bahama Ids., and Bermuda. However, Voss (1960: 420) found no *L. pealei* in collections from Bermuda; he also suggested that those squid from Bermuda listed as *L. pealei* by Verrill might have been *L. plei*. All 10 of the Bermuda *Loligo* specimens in the collection of the National Museum of Natural History are *L. plei*. Voss (1955: 83) listed *L. pealei* as recorded from Cuba by other sources but did not give the sources. LaRoe (1967: 23) gave the range of *L. pealei* as Massachusetts to Colombia, but also listed *L. pealei* from the islands cited by Voss. All of LaRoe's records from islands were citations from other authors which were not listed in his literature citations. All of the specimens examined and identified by LaRoe were from the continental shelf or slope. I have been unable to find evidence in the literature that *L. pealei* lives anywhere but on the continental shelf and upper slope. In searches of the collections at the University of Miami (in 1970 and 1973) and the Smithsonian Institution (1970-73) I found only 2 samples of *L. pealei* collected from island areas. These are 2 males from Eleuthera, Bahamas, and 3 males from Bridgetown, Barbados (USNM collections). These islands, although oceanic, are not distant from continents. I believe that these 5 squid represent rare strays and that *L. pealei* normally lives only on the continental shelf and slope.

It has been easiest for me to obtain large samples from waters between Beaufort, North Carolina, and Cape Cod, but this could be due to factors other than relative abundance. *Loligo pealei* is common to abundant on the continental shelf off the E coast of the United States (Serchuk & Rathjen, 1974); the remainder of the range of *L. pealei* has not been as intensively surveyed yet. According to LaRoe (1967), *L. pealei* is most common in the New England area. Only scattered individuals occur in the Gulf of Mexico and Caribbean Sea, according to Arnold et al. (1974), citing LaRoe (1967) and a personal communication from Mercer. No evidence has been given to support this statement. I examined 1 lot of 20 specimens from a station in the Gulf of Mexico and 1 lot of 163 specimens from the Caribbean (Table 6; Appendix A). Samples of more than 2-3 specimens from either Florida coast were not available and *L. pealei* probably is uncommon there. *L. pealei* has been found chiefly where the continental shelf is broad, with one exception—the coast of Colombia.

Loligo pealei is fished off the E coast of the United States by Canada, Spain, Italy, Cuba, West Germany, East Germany, USSR, Poland, the United States and others (Vovk, 1969; Rathjen, 1973). Japanese trawlers have averaged 10 or more tons per fishing day (Rathjen, 1973). About 90% of the New England squid catch is *L. pealei* (Summers, 1967). The total New England squid catch for 1973 was about 56,000 tons (123 million lb.) (Lux, Handwork & Rathjen, 1974). U.S. fishermen in 1973 caught well over 2 million lbs. (Rathjen, 1974). The fall apparent total abundance is calculated to average 60 thousand tons (Serchuk & Rathjen, 1974).

The distribution of populations of *Loligo pealei* in the western North Atlantic Ocean between Cape Hatteras and Nova Scotia has been analyzed from the results of year-round trawling studies or surveys by Summers (1969, 1971), Vovk (1969) and Serchuk & Rathjen (1974). Vovk's report is based on 3,420 trawls made during 24 expeditions between 1958 and 1968. Summers based his analysis on 4 cruises made between 1966 and 1968. Serchuk & Rathjen based their findings on 2,537 otter trawl stations from 1967-1971.

Populations of *Loligo pealei* occur in shallow waters of the continental shelf from Cape Hatteras to Cape Cod in summer months when spawning takes place. In fall, the species is dispersed in waters less than 110 m deep (Serchuk & Rathjen, 1974). Summers (1969), Vovk (1969) and Serchuk & Rathjen (1974) have shown that autumn populations migrate offshore into the deeper waters of depressions in the continental slope. The autumn offshore migration takes place at later dates at localities farther S. Furthermore, the northern limit of distribution occurs 600 km farther S in winter than in summer (Summers, 1969). Probably the inshore-offshore and N-S migrations are related to the avoidance of water temperatures of 8°C or lower (Summers, 1969). Vovk (1969) correlated concentrations to temperatures between 9-12°C in the depressions of the continental slope. In winter, bottom temperatures are higher there than on the continental shelf. Serchuk & Rathjen (1974) confirmed the findings of Summers and Vovk and found that in all seasons the best catches of squid were consistently made at locations where the temperature was above 10°C (10-12°C in spring and 10-14°C in fall) and are greatly diminished in strata with bottom temperatures below 8°C.

In mid-winter, populations of *Loligo pealei* are caught at depths between 28-366 m with peak abundance at 110-183 m; larger squid predominate with increasing depth (Summers, 1969; Serchuk & Rathjen, 1974). In spring relatively large concentrations of squid occur at 111-183 m; they are seldom taken in less than 55 m and never obtained in shallow waters N of Chesapeake Bay (Serchuk & Rathjen, 1974).

Populations of *Loligo pealei* are caught in canyons S of 40° N latitude from December to January at greater depths between Hudson and Veatch canyons than in the more southern canyons. Between March and May the greatest concentrations shift northward from Baltimore to Wilmington to Hudson and later Veatch and Hydrographer canyons (Vovk, 1969).[2] The squid leave the canyons in summer and migrate inshore to spawn.

Fertilized eggs of *Loligo pealei* in southern New England are deposited in masses from June to September; peak deposition takes place in June and July. Egg masses have been found attached to seaweed or other supports near Woods Hole (Verrill, 1874) and to wooden shipwrecks at a depth of 240 m off New Jersey (Bulloch, 1969). According to Summers (1971), hatching occurs mainly in July and November. Young *L. pealei* are very abundant in the surface waters off southern New England during July and August (Verrill, 1874). The newly hatched young closely resemble the adults and do not undergo metamorphosis. The juveniles are planktonic; the adults are nektonic.

Loligo pealei is generally demersal but disperses upwards into the water column at night; adults are observed swimming near the surface at night in summer (Summers, 1969). Daytime catches are about 9 times larger than nighttime catches; at night the squid may leave the bottom to pursue food (such as euphausids) which are known to migrate in a similar fashion (Serchuk & Rathjen, 1974). Recently hatched squid gather at the surface of an aquarium attracted by light.

The many other studies of *Loligo pealei* include: embryology (Arnold, 1964, 1965a, 1965b, 1965c, 1968a, 1968b, 1971), developmental rate (McMahon & Summers, 1971), spermatophores (Drew, 1919; Austin, Lutwak-Mann & Mann, 1964), breeding behavior (Drew, 1911; Arnold, 1962), morphology compared with *Lolliguncula brevis* (Haefner, 1964; Dillon & Dial, 1962), anatomy (Verrill, 1881; Williams, 1909), breeding seasons and growth rates (Summers, 1968, 1971), maturity (Vovk, 1972b), feeding habits (Vovk, 1972a), useful manual of laboratory techniques (Arnold et al. 1974), chromatophores (Mirow, 1972), locomotion (Ward, 1972).

Loligo pealei has been captured in the same bottom trawls (not closing nets) with *L. plei* and *L. roperi* as shown in Table 3.

Sexual dimorphism: Analysis of covariance showed that the sexes are significantly different statistically in many characters, but these differences are very small and graphed values overlap. Sexual differences are distinctive in only 2 characters: females have a broader gladius vane and fewer gill filaments than do males. See Figs. 5 and 6.

Tests of sexual differences using ML as covariate sometimes showed statistically significantly different variances between male and female samples. When the tests were repeated using specimens of only 120-200 mm ML, the variances were then not significantly different.

When either ML or the length of the funnel cartilage is used as the covariate, the adjusted means for the following measure-

TABLE 3. Location of trawls containing 2 or more loliginid species.

Collector, sta. no.	Location	Date	*Loligo ocula*	*Loligo pealei*	*Loligo plei*	*Loligo roperi*	*Lolliguncula brevis*
Choco 38	9°3.5′N, 76°28′W	18 May 1969		x	x	x	
J. Ewald	Gulf of Venezuela	2 Mar. 1971		x	x		
Delaware II							
D-72-25 9	34°39′N, 75°39′W	27 Oct. 1972		x	x		
D-72-25 4	35°11.5′N, 75°12′W	27 Oct. 1972		x	x		
D-72-25 24	34°13′N, 76°53′W	29 Oct. 1972		x	x		
J. Ewald	Gulf of Venezuela	1 Mar. 1971			x		x
Oregon II							
10858	22°59′N, 78°43′W	13 Dec. 1969	x			x	
Pillsbury							
406	8°49.2′N, 77°21.2′W	17 July 1966		x		x	
352	8°20.1′N, 76°53.6′W	11 July 1966		x		x	

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[2] Black and Witch Canyons mentioned in the translation of Vovk's paper are probably mistranslations of Block and Veatch Canyons, which appear on Coast and Geodetic Survey Maps (1967) of the region.

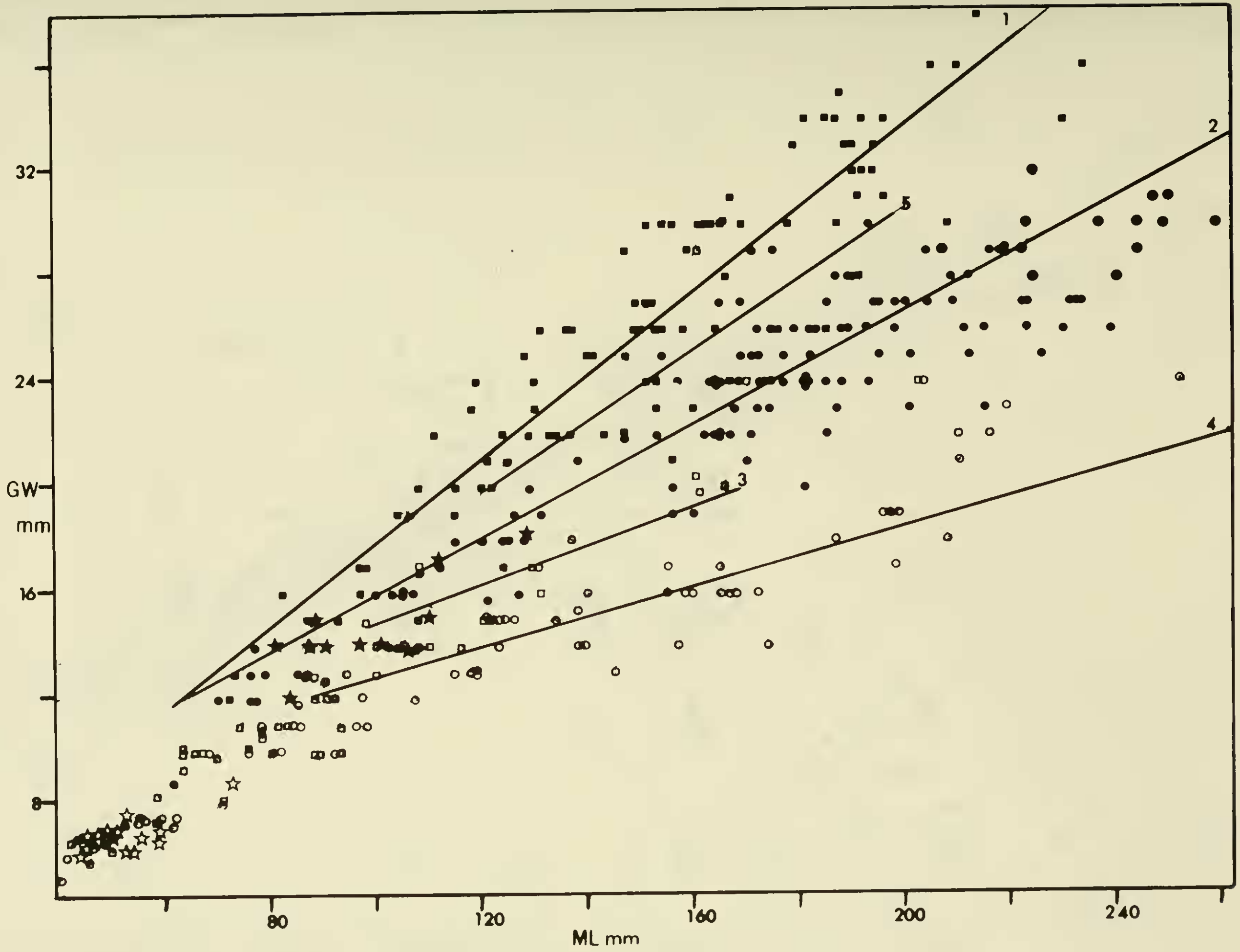

FIG. 5. The regression of greatest width of gladius upon mantle length (GW:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei* ♀ = open squares, regression line no. 3; ♂ = open circles, regression line no. 4. *L. ocula* = solid stars. *L. roperi* = open stars. *L. pealei* 120-200 mm ML only (used to test sexual dimorphism), regression line no. 5.

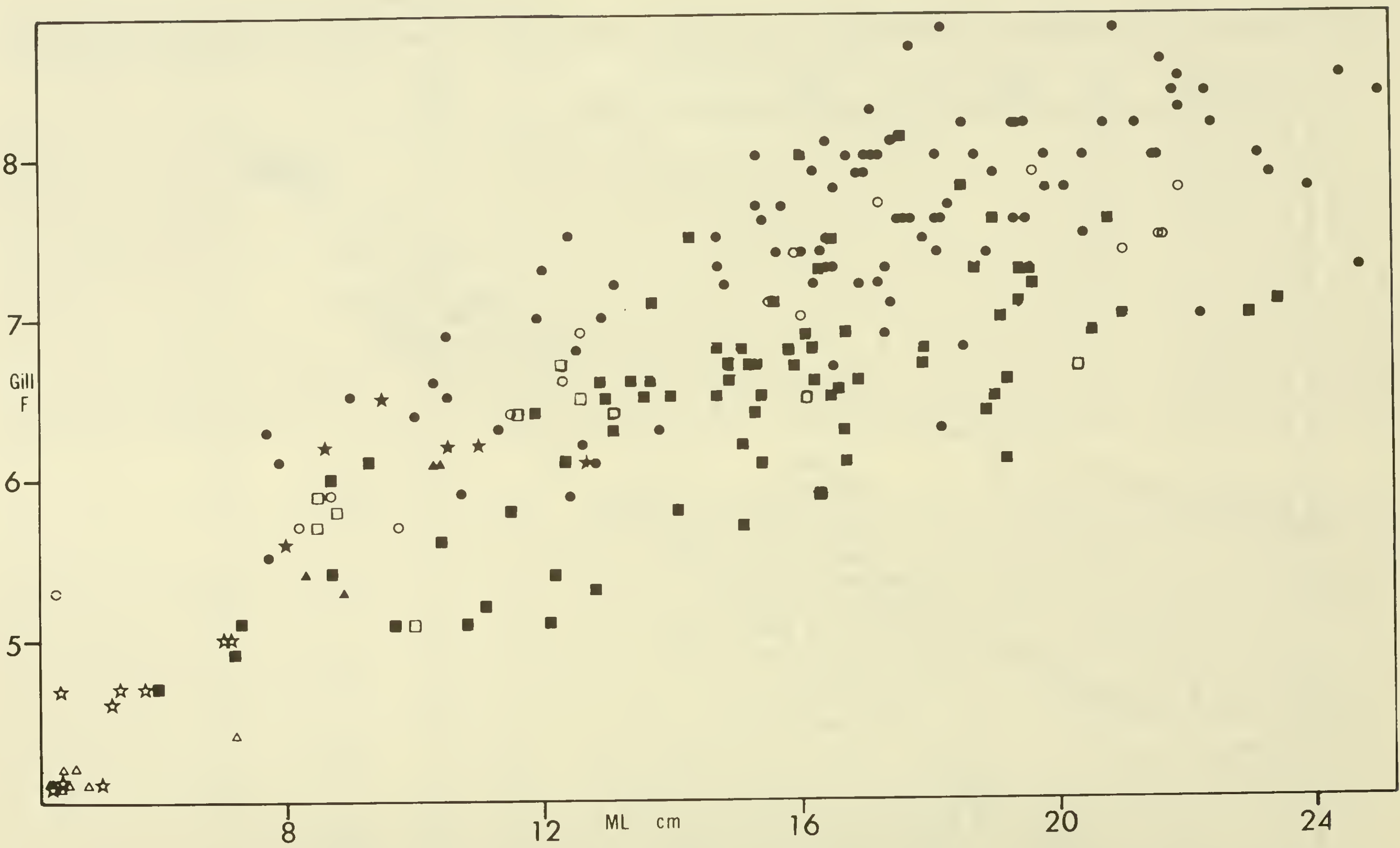

FIG. 6. The regression of the number of gill filaments upon mantle length (Gill F:ML). *Loligo pealei*: ♀ = solid squares, ♂ = solid circles. *L. plei*: ♀ = open squares, ♂ = open circles. *L. ocula*: ♀ = solid triangles, ♂ = solid stars. *L. roperi*: ♀ = open triangles, ♂ = open stars.

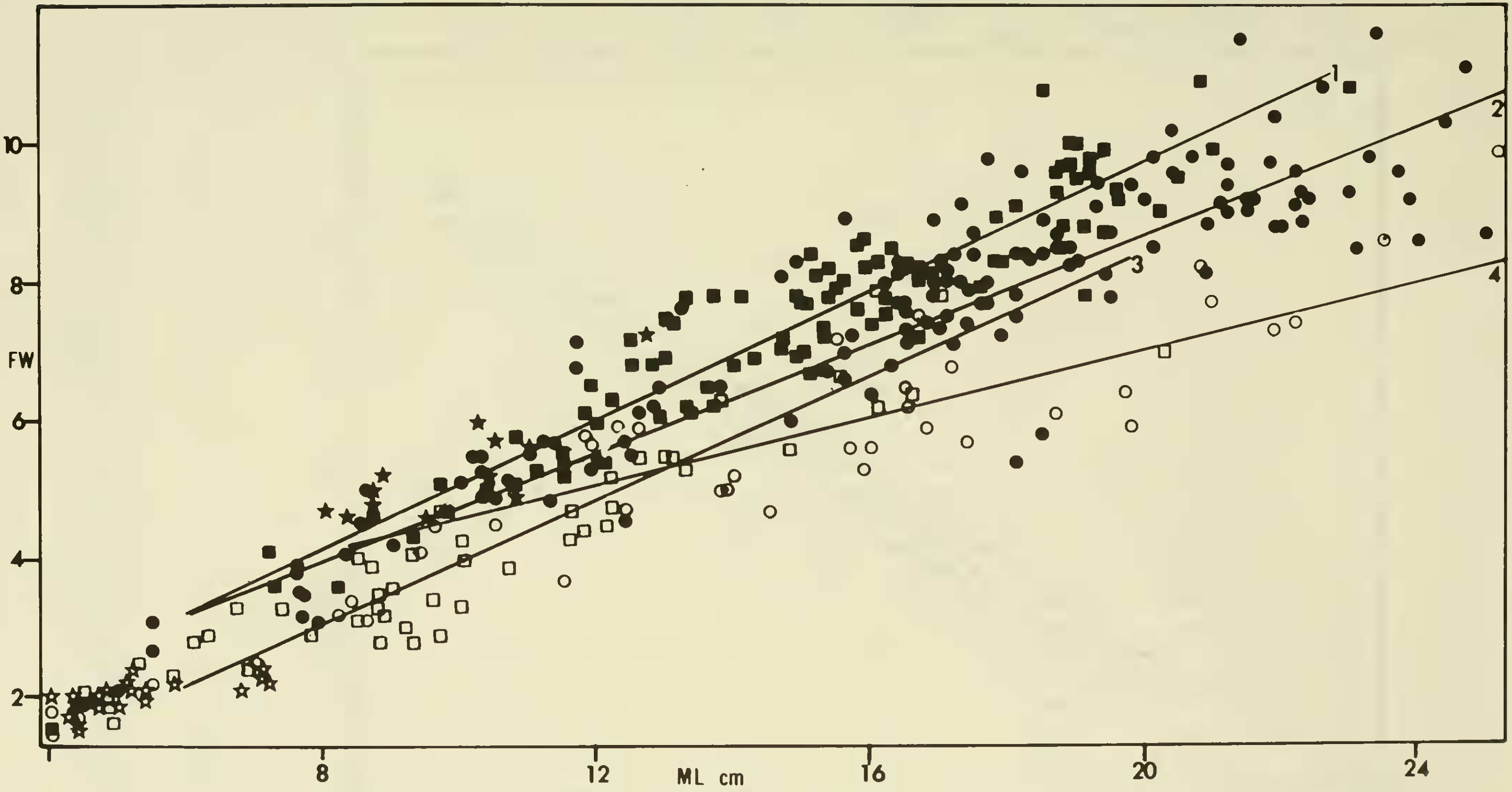

FIG. 7. The regression of fin width upon mantle length (FW:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei*: ♀ = open squares, regression line no. 3; ♂ = open circles, regression line no. 4. *L. ocula* = solid stars. *L. roperi* = open stars.

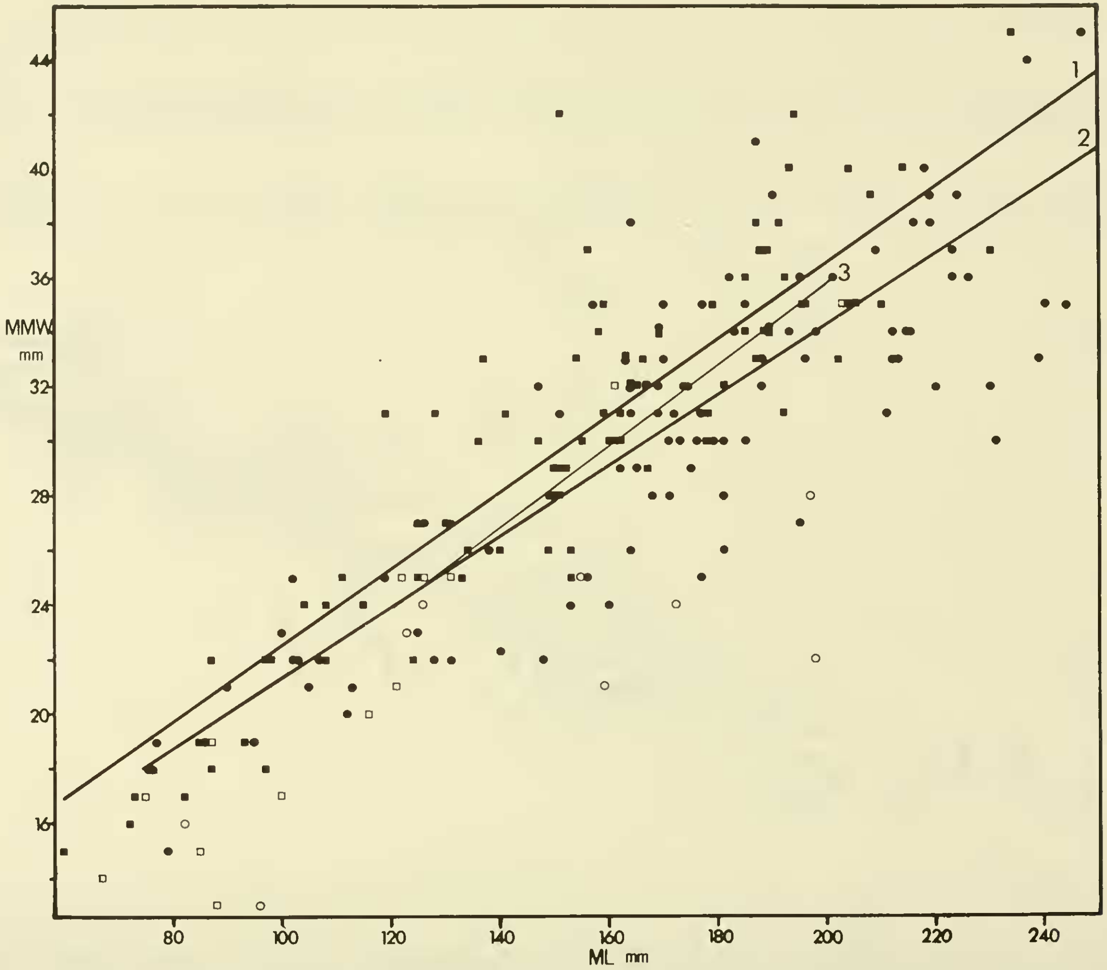

FIG. 8. The regression of mid-mantle width upon mantle length (MMW:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei*: ♀ = open squares, ♂ = open circles. *L. pealei* 120-200 mm ML only, regression line no. 3.

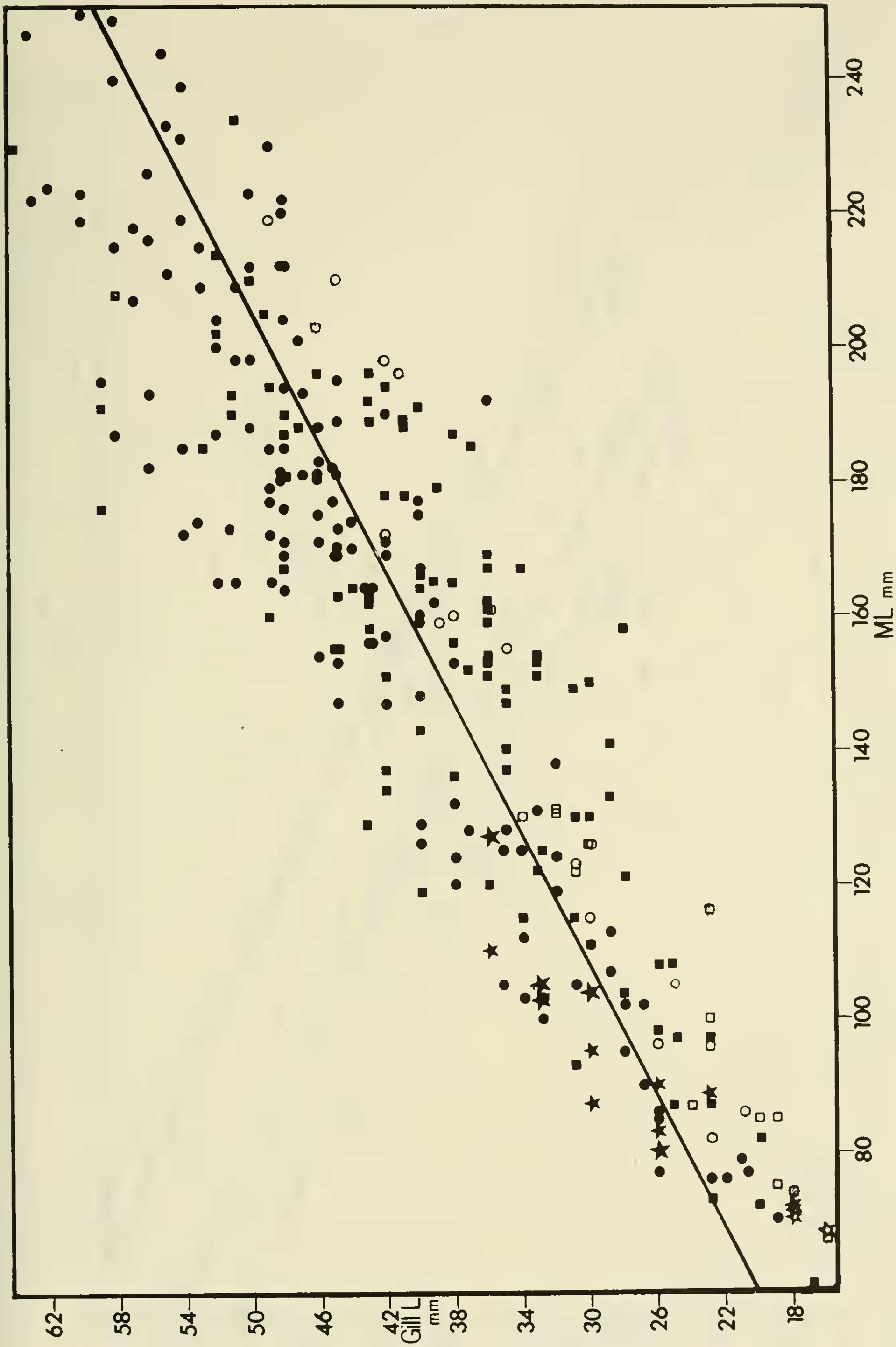

FIG. 9. The regression of gill length upon mantle length (Gill L:ML). *Loligo pealei*: ♀ = solid squares, ♂ = solid circles. *L. plei*: ♀ = open squares, ♂ = solid circles. *L. ocula*: solid stars. *L. roperi*: open stars. Regression line for *L. pealei* only.

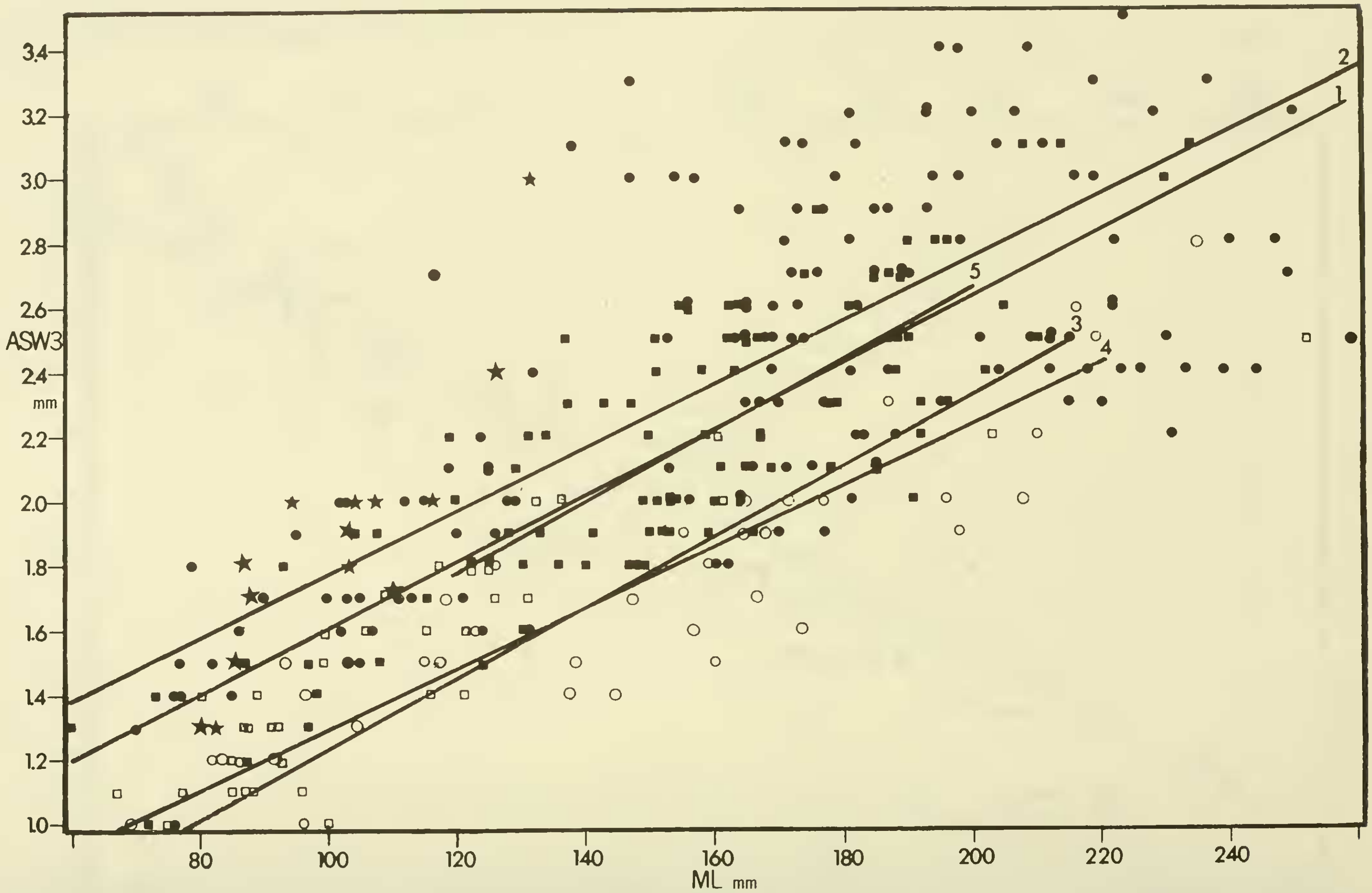

FIG. 10. The regression of the greatest sucker width of arm III upon mantle length (ASW III:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei*: ♀ = open squares, regression line no. 3, ♂ = open circles, regression line no. 4. *L. ocula* = solid stars. *L. roperi* = open stars. *L. pealei* 120-200 mm ML only, regression line no. 5.

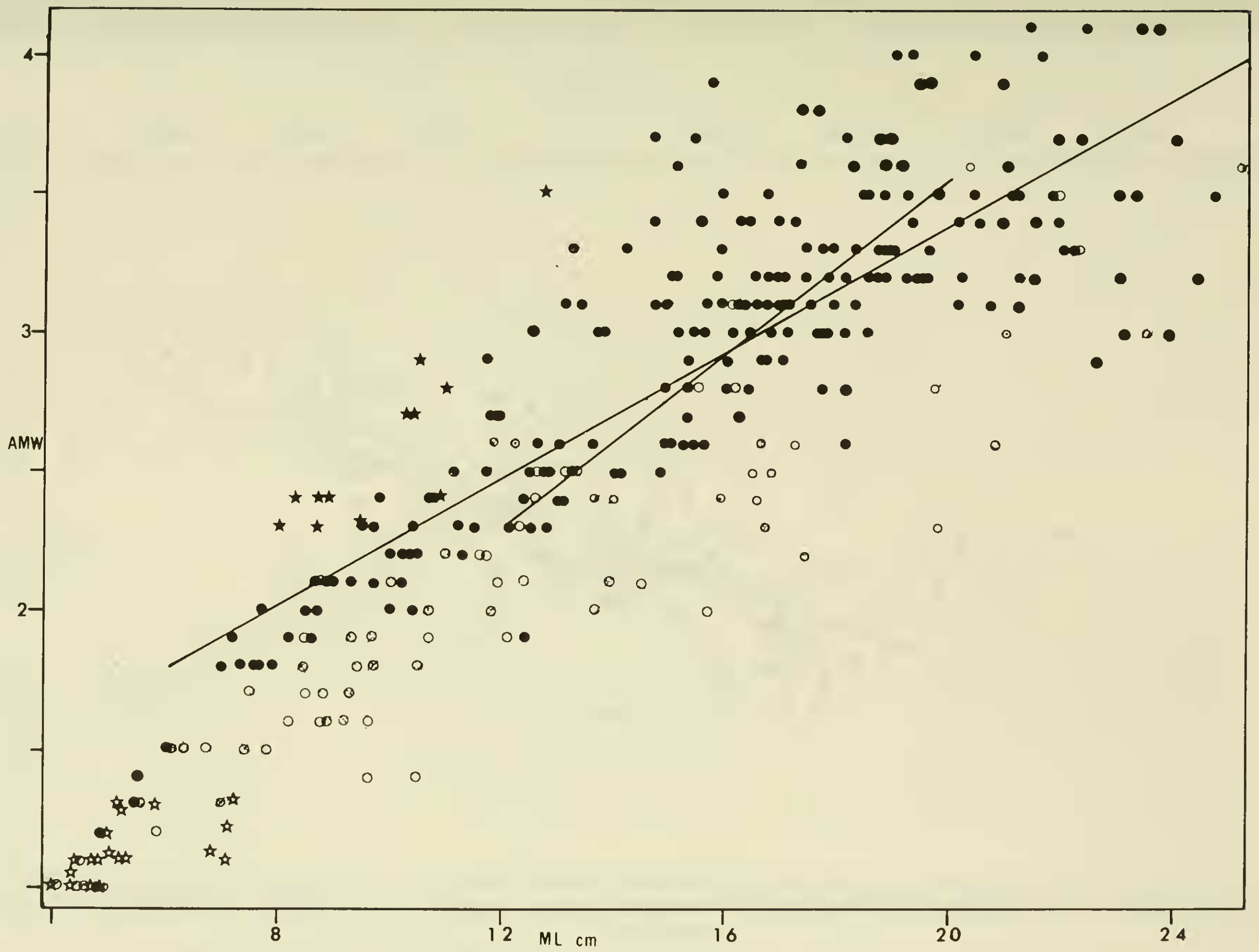

FIG. 11. The regression of anterior mantle width upon mantle length (AMW:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars. Both regression lines for *L. pealei* (short line used to test sexual dimorphism).

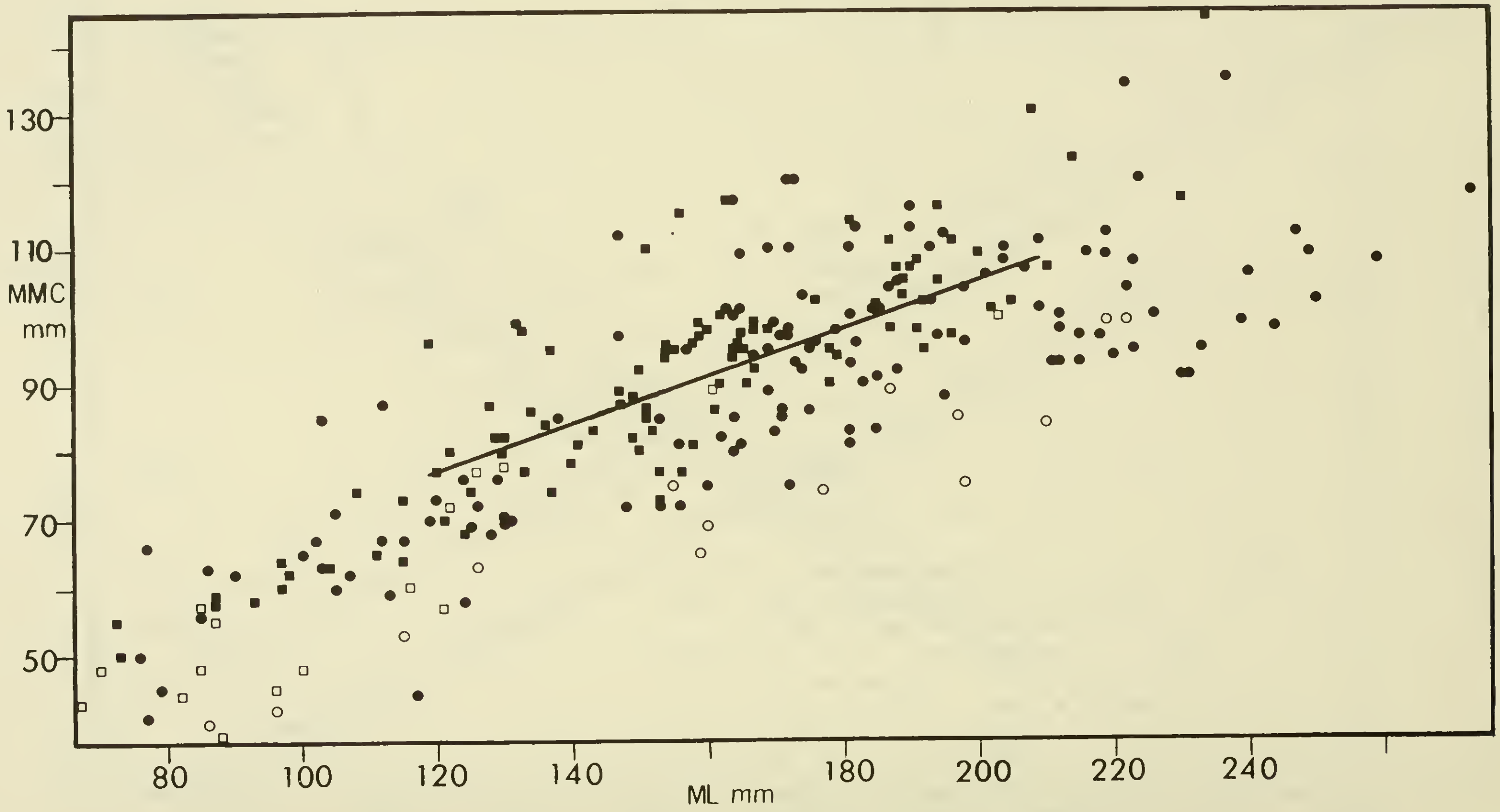

FIG. 12. The regression of mid-mantle circumference upon mantle length (MMC:ML). *Loligo pealei*: ♀ = solid squares, ♂ = solid circles. *L. plei*: ♀ = open squares, ♂ = open circles. Regression line for *L. pealei* only.

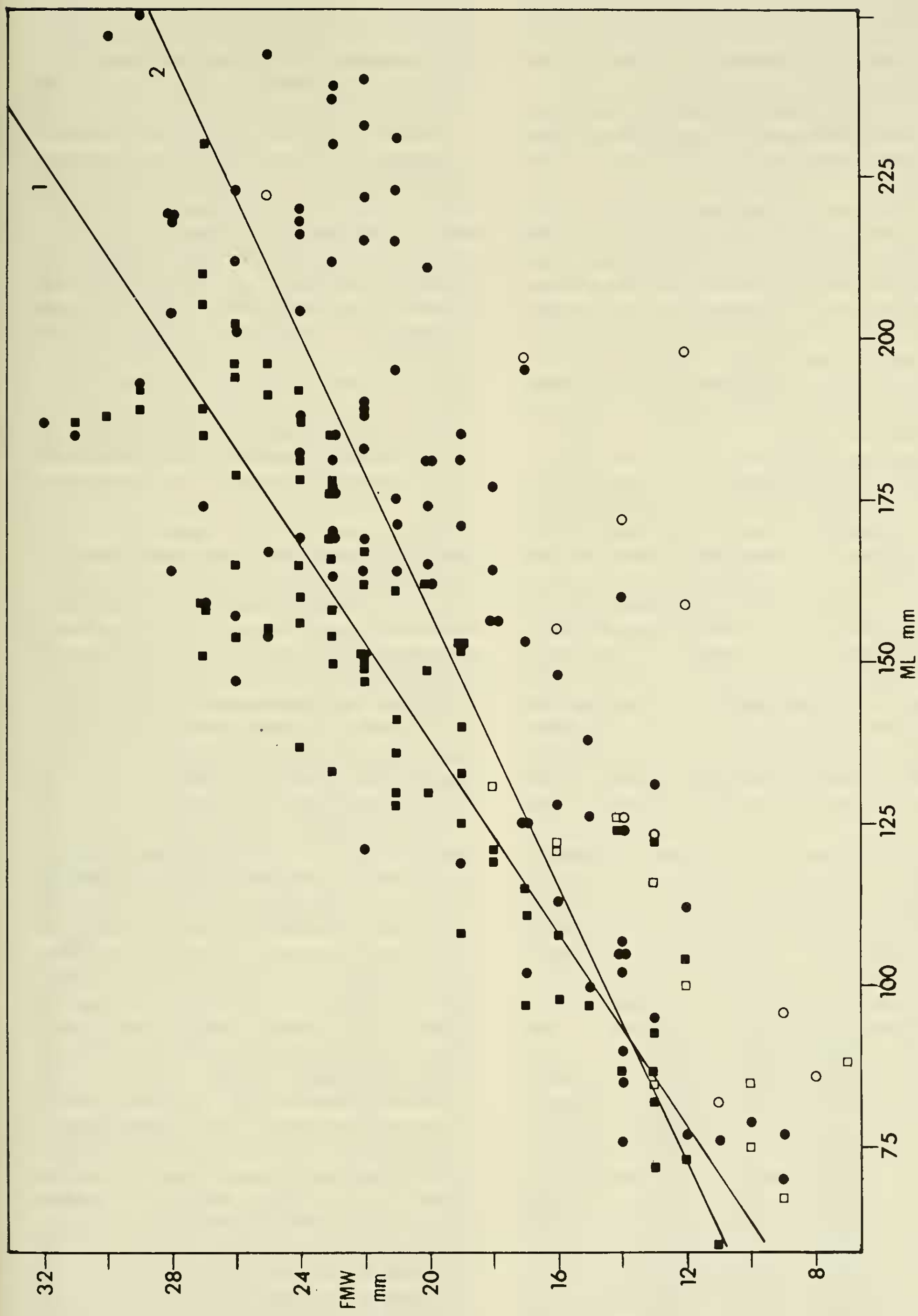

FIG. 13. The regression of mantle width coincident with widest point of fins upon mantle length (FMW:ML). *Loligo pealei*: ♀ = solid squares, regression no. 1; ♂ = solid circles, regression no. 2. *L. plei*: ♀ = open squares, ♂ = open circles.

ments are statistically significantly higher in females than in males: fin width, mid-mantle width, gladius width; and the following show statistically significantly higher means in males than in females: gill length, the number of gill filaments, and the widths of the suckers on arms II, III, and IV. See Figs. 7-10. The differences are most pronounced in gladius width and the number of gill filaments.

In addition, regression coefficients are statistically significantly different for fin width and the width of the mantle at mid-fin length, when ML is used as the independent variable. These 2 characters increase faster in respect to increasing ML in females than they do in males. Females appear to have a higher regression coefficient also for gladius width:ML, but variance differences made a statistical test invalid.

There are probably no real differences in mantle width between the sexes except posterior to the fin insertion. While mid-mantle width:ML shows significant difference between the sexes, regressions on ML of mid-mantle circumference, as well as anterior mantle width and circumference do not (Figs. 11-12). There is considerable overlap between the sexes in these characters. Mid-mantle circumference is a more accurate measurement than mid-mantle width. The higher regression of mantle width at mid-fin length:ML in females is probably due to swelling of the posterior part of the mantle with eggs in mature ripe females (Fig. 13).

With the length of the funnel cartilage as covariate (but not with ML as covariate) females have higher adjusted mean head width and nuchal cartilage length, and males have higher adjusted mean fin length, arm I length and arm I sucker width. Broad overlap of values occurs in these characters.

No sexual dimorphism occurs in the following measurements using either ML or length of the funnel cartilage as covariates: head length, distance between the eyes, funnel length, funnel width, tentacular club length, tentacular sucker width, length of arms II, III, IV, and number of suckers on each arm. While there is a low correlation between the number of suckers on arms and ML, the analysis of covariance showed that the regression is significant. No sexual dimorphism is observed in the teeth of the largest suckers on either the third arm or the tentacular club.

More males than females have a longitudinal mid-ventral ridge and it is more pronounced in males. Some large mature males have longitudinal, reddish-brown chromatophore stripes extending posteriorly near the ventro-lateral margins of the mantle opening.

Verrill (1881: 314-316) examined many specimens of *Loligo pealei* from between Long Island Sound and Cape Ann, Massachusetts, and he reported that the gladius is wider in females than in males. In mature females the broad portion of the gladius lies above the full ovary and may help support or protect the large mass of eggs in a ripe female. Verrill stated that the ratios of head circumference to ML, fin width to ML, tentacular sucker width to ML and arm I length to ML are larger in females than males. While the ratios varied he found no overlap between sexes for these ratios with the exception of tentacular sucker width to ML.

Testing for sexual dimorphism in all geographic samples of *Loligo pealei* together, I found that the mean of fin width adjusted for ML is indeed statistically significantly larger in females than in males, but with considerable overlap (Fig. 7). There is no statistically significant difference for head width:ML; tentacular sucker width:ML; and arm I length:ML. Males have longer 1st arms than females using length of funnel cartilage as covariate, but values overlap so much that this is not apparent on a graph.

Verrill asserted, without giving the figures, that all arms are longer and all of the suckers usually distinctly larger in females. There is no statistically significant difference in the lengths of arms II, III, IV, and males have longer 1st arms and larger suckers (Fig. 10). Verrill felt that preservation changes might mask sexual dimorphism. However, preservation probably affects most characters of males and females alike, altering ratios and regressions alike.

Females have shorter gills with fewer filaments than males which suggests that females may have a lower oxygen requirement. Males are more active in mating (Drew, 1911; Arnold, 1962), but females produce and lay 3500-6000 eggs (Summers, 1971). Other relative differences in activity are not now known for the 2 sexes.

Maturity and growth: The smallest male found with spermatophores was 61 mm ML (*CHOCO* station 38, off Colombia, May 18,

1969) and the largest without spermatophores was 219 mm ML (*A.E. VERRILL*, Martha's Vineyard, Massachusetts, Oct. 8, 1970). The smallest female found with eggs was 73 mm ML (*OREGON II* station 223, off Colombia, Nov. 28, 1968) and the largest found without eggs was 208 mm ML (*A.E. VERRILL,* Martha's Vineyard, Massachusetts, Oct. 8, 1970). The relationship of maturity to water temperature will be discussed under geographic variation.

The hectocotyli of 126 males (49-315 mm ML) were examined. Males as large as 54 mm ML (*CYNTHIA*, off Virginia, May 18, 1971) have no hectocotylus. Partial hectocotylization is present in immature males as small as 47 mm ML (*PILLSBURY* station 352, off Colombia, July 11, 1966) and as large as 76, 85, and 90 mm ML (*CYNTHIA*, off Virginia, June 15, 1971). In the last 3 specimens about 6 suckers on the dorsal row are 1/2 the diameter of their partners on the ventral row and their stalks are more elongate. The dorsal suckers in the region of the future hectocotylus are like their ventral partners on the left arm IV of small males (less than ca. 45-70 mm ML). The hectocotylus appears to be formed by differential growth of the dorsal suckers in the future region of the hectocotylus.

Within the ML range considered in this study (60-315 mm), many measured characters do not appear to change much in size with increasing ML. Although these correlations are very low, all except the number of transverse rows of tentacular suckers are statistically significant for the sample size (Tables 4-5), which means that these characters do increase slightly with increasing ML within the range considered.

Many measured characters show high correlations (Table 5). The lengths of the arms and tentacular club and sucker diameters are all highly correlated with each other. The mantle width and head width appear similarly related. That these correlated characters may not be independent of each other should be considered when making comparisons between animals. These correlations could represent common genetic control.

A few abnormalities were noted in the arrangement of arm suckers in *Loligo pealei*. A total of 215 arms was examined. In a female (154 mm ML, Martha's Vineyard, Massachusetts, July 1971) the sucker-bearing surface of the right arm II is interrupted in one place by a convergence of the 2 lateral epidermal surfaces across the suckered ventral surface of the arm. In a female (150 mm ML, *CYNTHIA*, off Virginia, May 18, 1971) the biserial arrangement of suckers on the right ventral arm is replaced in 4 suckers near the basal portion of the arm with a left, right, right, left arrangement. A total of 119 arms was examined. A male (315 mm ML) *CYNTHIA*, off Virginia, May 18, 1971) has a hectocotylized arm with 3 suckers instead of 2 in one row at one point on the arm. A total of 118 hectocotyli were examined. Bradbury & Aldrich (1971) observed this arrangement in a specimen of *Illex illecebrosus*.

Abnormal numbers of buccal lappets and other variations in the hectocotylus were also observed and are discussed next under geographic variation.

Geographic variation: Eleven samples of populations of *Loligo pealei* from 5 geographic areas were statistically analyzed for geographic variation. The samples are listed in Table 6 and shown as stars in Fig. 1. Comparison was made of more than 50 different counts, measurements or observations. Most of these are listed in the description of measurements. When the study had been partially completed the following measurements were no longer made for an entire population sample but for only 10 specimens (5 males and 5 females) in each sample: distance between the eyes; anterior and mid-mantle widths; mantle width at fin insertion; number of suckers on arms I, III, IV; width of suckers on arms I, II, IV, and

TABLE 4. Some characters in *Loligo pealei* with a correlation of less than 0.6 with mantle length.

Character	Mantle length		Funnel cartilage length	
	r	N	r	N
TSR	0.214	76	0.749	73
TL	0.312	221	0.491	218
BLS 7	0.347	116	0.355	115
1	0.318	117	0.287	116
2	0.397	118	0.477	117
3	0.264	118	0.318	117
4-5	0.440	117	0.417	116
6	0.322	117	0.338	116
Fun W	0.428	217	0.553	217
HAS	0.400	118	0.514	117
HS	0.321	118	0.353	117
AS I	0.568	115	0.705	114
II	0.555	215	0.679	214
III	0.585	119	0.706	118
IV	0.356	119	0.492	118
TCL	0.598	220	0.725	216
Gill W	0.517	172	0.618	171

TABLE 5. Correlations greater than 0.8 between measurements of *Loligo pealei* (sample sizes in parentheses).

	ML	FCL	NCL	FL	FW	HW	MWA
ML		0.915(232)	0.924(228)	0.994(232)	0.924(175)	0.832(225)	0.838(196)
FCL	0.915(232)		0.943(228)	0.897(228)	0.904(226)	0.904(225)	0.891(192)
NCL	0.924(228)	0.943(228)		0.911(224)	0.885(222)	0.892(221)	0.877(188)
FL	0.994(232)	0.897(228)	0.911(224)		0.917(175)		0.821(192)
FW	0.924(175)	0.904(226)	0.885(222)	0.917(175)			
HW	0.832(225)	0.904(225)	0.892(221)				0.892(191)
AMW	0.838(199)	0.891(192)	0.877(188)	0.821(192)			
MMW	0.852(179)	0.891(175)	0.889(171)	0.839(175)		0.872(175)	0.899(179)
AMC	0.843(228)	0.903(228)	0.907(224)	0.825(224)	0.864(222)	0.922(221)	0.924(118)
MMC	0.809(225)	0.885(225)	0.874(221)		0.871(220)	0.892(218)	0.900(185)
Gill L	0.891(232)	0.869(228)	0.889(226)	0.875(228)		0.809(225)	0.816(193)
GW	0.785(217)*	0.830(216)			0.861(210)	0.810(210)	0.803(179)
AL I							
II							
III		0.822(218)	0.816(214)				
IV							
ASW I		0.834(130)	0.820(126)			0.838(129)	0.817(123)
II						0.816(129)	
III		0.818(230)	0.821(226)			0.857(227)	0.844(196)
IV						0.803(129)	

	MWM	MCA	MCM	Gill L	GW	AL I	AL II
ML	0.852(179)	0.843(228)	0.809(225)	0.891(232)			
FCL	0.891(175)	0.903(228)	0.885(225)	0.869(228)	0.830(216)		
NCL	0.889(171)	0.907(224)	0.874(221)	0.889(226)			
FL	0.839(175)	0.825(224)		0.875(228)			
FW		0.864(222)	0.871(220)		0.861(210)		
HW	0.872(175)	0.992(221)	0.892(218)	0.809(225)	0.810(210)		
AMW	0.899(179)	0.924(118)	0.900(185)	0.816(193)	0.803(179)		
MMW		0.907(171)	0.929(169)	0.812(176)	0.836(162)		
AMC	0.907(171)		0.951(225)	0.849(224)	0.811(212)	0.812(214)	0.854(221)
MMC	0.929(169)	0.951(225)		0.801(221)	0.819(209)		
Gill L	0.812(176)	0.849(224)	0.801(221)				
GW	0.836(162)	0.811(212)	0.819(209)				
AL I		0.812(214)					0.96(87)
II		0.854(221)				0.96(87)	
III	0.815(166)	0.875(214)	0.808(211)	0.823(215)		0.953(210)	0.96(87)
IV		0.862(213)				0.96(87)	0.971(213)
ASW I		0.862(126)	0.817(126)			0.866(118)	0.884(127)
II		0.826(126)				0.906(118)	0.903(127)
III		0.861(226)		0.811(230)		0.918(216)	0.915(224)
IV		0.824(126)				0.876(118)	0.871(127)

	AL III	AL IV	ASW I	ASW II	ASW III	ASW IV
ML						
FCL	0.822(218)		0.834(130)		0.818(230)	
NCL	0.816(214)		0.820(126)		0.821(226)	
FL						
FW						
HW			0.838(129)	0.816(129)	0.857(227)	0.803(129)
AMW			0.817(123)			
MMW	0.815(166)					
AMC	0.875(214)	0.862(213)	0.862(126)	0.826(126)	0.861(226)	0.824(126)
MMC	0.808(211)		0.817(126)			
Gill L	0.823(215)				0.811(230)	
GW						
AL I	0.953(210)		0.866(118)	0.906(118)	0.918(216)	0.876(118)
II	0.96(87)	0.971(213)	0.884(127)	0.903(127)	0.915(224)	0.871(127)
III		0.975(208)	0.896(120)	0.900(120)	0.922(219)	0.881(120)
IV	0.975(208)		0.883(118)	0.900(118)	0.925(216)	0.881(118)
ASW I	0.896(120)	0.883(118)		0.952(134)	0.944(134)	0.948(134)
II	0.900(120)	0.900(118)	0.952(134)		0.966(134)	0.952(134)
III	0.922(219)	0.925(216)	0.944(134)	0.966(134)		0.941(134)
IV	0.881(120)	0.881(118)	0.948(134)	0.952(134)	0.941(134)	

*Male GW = 0.819(126); female GW = 0.909(88).

TABLE 6. Samples of *L. pealei* used for statistical analysis.

Sample no.	N	Location	Date	Depth m	Collector, no.	Specimen,* no.
1	17	Menemsha Bight, Martha's Vineyard, Mass.	30 July 1970	7	Cohen, *Captain Bill IV*	1-17
3	14	Menemsha Bight, Martha's Vineyard, Mass.	4 Sept. 1969	20	Summers, *A. E. Verrill*	18-28, 54-56
4	24	Vineyard Sound, Mass.	8 Oct. 1970	13-15	Summers, *A. E. Verrill*	70-93
12	30	Vineyard Sound, Mass.	14 July 1971	—	*Captain Bill IV*	242-271, 280
13	44	37°50-55′N, 75°10-20′W	18 May 1971	8-20	Cohen, *Cynthia,* 1-3	272-279, 281-316
20	17	37°50′N, 75°10′W	15 June 1971	20	Sweeney, *Cynthia,* 3	323-339
8	28	4 mi. S of Beaufort Bar, Beaufort, N.C.	24 Sept. 1970	13	Schwartz, *Machapunga*	160-187
2	20	29°29′N, 88°37′W	26 Jan. 1970	8	*Oregon II,* 10886	29-48
9	11	9°37′N, 76°01′W	28 Nov. 1968	10	*Oregon II,* 223	201-202
		9°45′N, 75°45′W	28 Nov. 1968	7	*Oregon II,* 219	203-208
		10°N, 75°44′W	27 Nov. 1968	11	*Oregon II,* 214	198-200
11	22	9°3.5′N, 76°28′W	18 May 1969	10	*Choco,* 38	190-197, 317-319
		9°31′N, 76°10.6′W	15 May 1969	10	*Choco,* 25	209-219
10	10	Gulf of Venezuela (NW)	2 Mar. 1971	—	J. Ewald	232-240

*All specimens are in the National Museum of Natural History (United States National Museum), Washington, D.C.

the tentacular club; number of gill filaments; and number of suckers on buccal lappets. Preliminary analysis indicated that these measurements were not useful enough for the purposes of this study to justify the time spent measuring them. Also mantle width is closely correlated with mantle circumference; distance between eyes with head width; number of suckers on arms I, III, IV with the number on arm II; and width of the suckers on arms I, II, IV with the width of the suckers on arm III.

Comparison of the first samples of populations from different geographic locations showed clinal differences in several characters. However, when I later examined new material, I found that 2 samples from the same locality often differ more from each other than they do from a sample from another locality. This is true of characters affected by differences in preservation as well as those unaffected by such differences. Table 7 shows some variables in which 2 samples from Woods Hole differed more from each other than from samples from other localities.

Only 2 characters show any statistically significant geographic variation: gill length

TABLE 7. Comparisons of adjusted means showing greater differences between samples of *Loligo pealei* from the same locality than from other localities.

Measurement	Covariate	Martha's Vineyard, Mass.				Other locality		
		Sample 4		Sample 12				
		$\bar{X}$ mm	N	$\bar{X}$ mm	N	$\bar{X}$ mm	N	
Gill L, F*	ML	43.2	11	33.4	11	35.1	7	Colombia
GW, F	ML	23.0	11	27.4	11	25.9	7	Colombia
ASW III, F	FCL	2.2	11	2.0	11	1.9	7	Colombia
AS II	ML	109	23	96	30	106	24	Beaufort, N.C.
FCL	ML	21.8	23	20.5	30	21.4	24	Beaufort, N.C.

*F = Female.

and the number of transverse sucker rows on the tentacular club. The regression coefficients of gill length on funnel cartilage length show a statistically significant difference ($p < 0.05$) between samples from the E coast of the United States and samples from the Gulf and Caribbean Sea (Fig. 14). Gill length increases faster relative to increasing funnel cartilage length in samples from the Gulf and Caribbean Sea than in samples from the U.S. E coast. Faster growth of gills may be correlated with a lower oxygen content in the waters of the warmer part of the range of *Loligo pealei*. Roper (1969) found correlations between increased gill size and number of filaments and lower oxygen concentrations for *Bathyteuthis* and noted that similar correlation had been found for some fish. However, increase in gill length also could be correlated with a

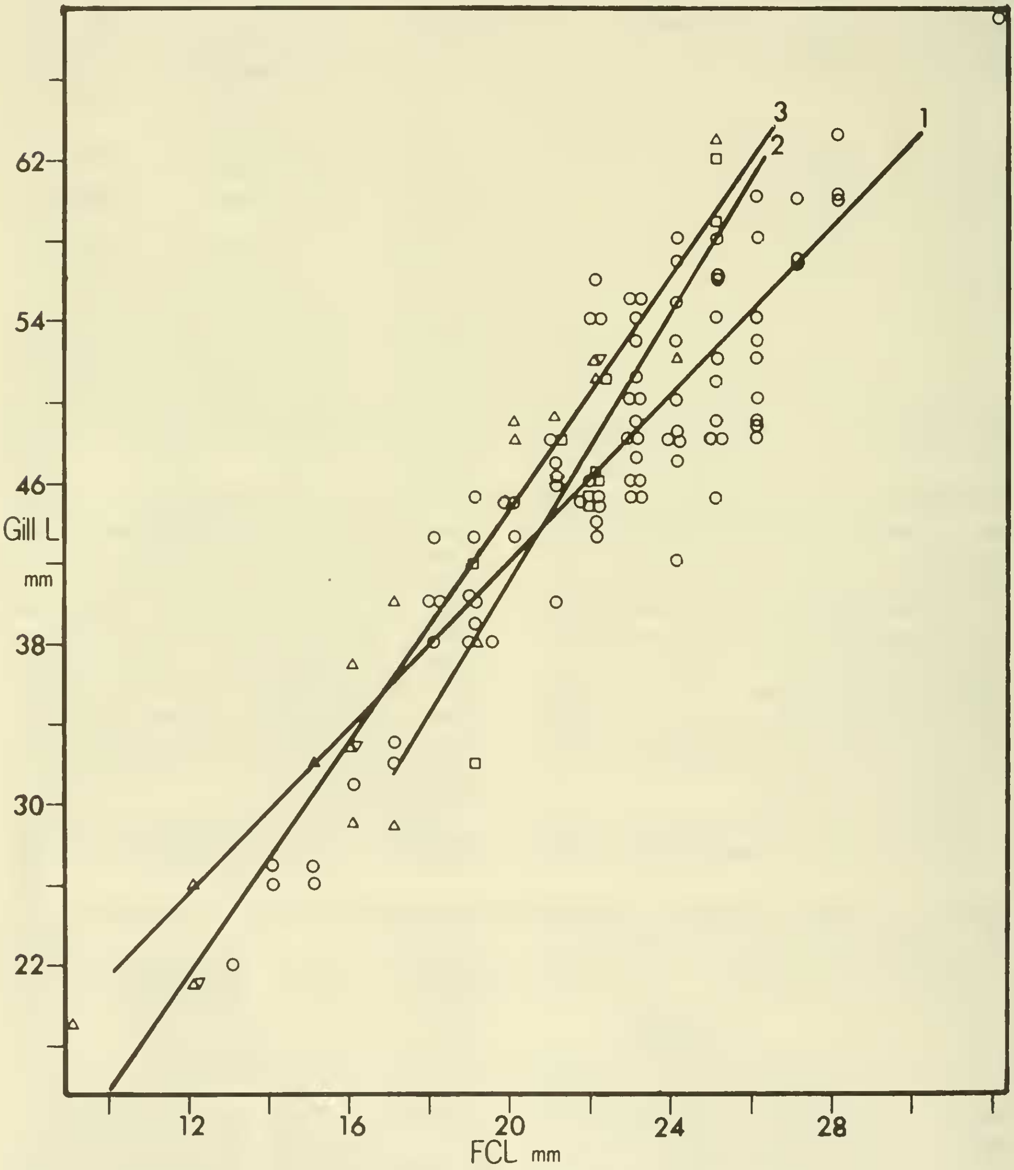

FIG. 14. The regression of gill length upon funnel cartilage length (Gill L:FCL) in males of *Loligo pealei*. Eastern coast of United States = open circles, regression no. 1. Gulf Coast of United States = open squares, regression no. 2. Caribbean Sea = open triangles, regression no. 3.

higher metabolic rate in warmer waters. Voss (1967) and Robson (1925) suggested that decreased respiratory surface in deep-sea octopods was correlated with lower temperature and lower metabolic rate. Walters (1961) suggested the same for some bathypelagic fishes.

It is surprising to find that the regression coefficient for Gill L:FCL is higher for the northern Gulf of Mexico sample than for the Caribbean samples. Ekman (1953) felt that the northern Gulf is more similar to warm temperate regions like Beaufort, North Carolina, than to the tropical Caribbean Sea. Intense cold spells have killed fishes in the northern Gulf about once every 14 winters (Leipper, 1954). On the other hand summer surface waters are about 28°C throughout the Gulf (Leipper, 1954). The regression of Gill L:FCL may be related more to summer temperatures than to winter ones or may be the result of the relatively smaller sample size tested.

In contrast to Gill L:FCL, the number of gill filaments in relation to ML appears to be lower in males (no large females available) from the Caribbean than in males from northern samples.

Table 8 shows a cline in the mean number of transverse sucker rows (TSR) on the tentacular club for samples of populations from the eastern Atlantic coast of the United States, northern Gulf of Mexico, and the Caribbean Sea. A significant difference ($p < 0.05$) exists only between the samples from the Caribbean versus the samples from the Gulf of Mexico and the eastern Atlantic coast of the United States. Furthermore, the means of smaller geographic regions are not perfectly arrayed in a cline and the standard deviations show that the geographic areas overlap in TSR (Table 9). Therefore, there is no meaningful geographical difference in TSR.

No other characters show geographical clines in means, means adjusted by covariance, or in regression coefficients. However the Caribbean samples differ from samples from other regions not only in gill length but also show increased variability, particularly in the hectocotylus. The hectocotylus is 1 of the 2 nonoverlapping characters differentiating *Loligo pealei* from *L. plei.* (Figs. 4, 20). In most *L. pealei* only 10-12 suckers in the dorsal row are hectocotylized; the rest of the distal dorsal suckers are equal in diameter to those in the ventral row. In *L. plei*, reduction of the suckers of the dorsal row extends to the tip of the arm. In all geographic samples of *L. pealei*, except the one from Beaufort, there are some specimens with more than 12 suckers somewhat reduced in diameter distal to the 10-12 hectocotylized suckers. The 3 Caribbean samples have the most specimens with greater reduction of the dorsal row (11 of 44 males).

TABLE 8. Possible geographic variation in number of sucker rows on the tentacular club of *Loligo pealei.*

Region	Sample size	Sucker rows		Significance
	N	$\bar{X}$	±S	
East Coast U.S.	63	38.4	1.99	
Gulf Coast U.S.	15	36.0	2.3	NS
Caribbean Sea	22	35.4	2.3	$P < 0.05$

TABLE 9. Possible geographic variation in number of sucker rows on the tentacular club of *Loligo pealei.*

Locality	Sample size	Sucker rows		Significance
	N	$\bar{X}$	±S	
Cape Cod, Mass.	61	39.1	2.3	
Assateague, Va.	20	38.6	1.6	NS
Beaufort, N.C.	11	38.6	2.2	NS
Venezuela	8	36.5	1.4	$P < 0.05$
Louisiana	16	36.1	2.2	NS
Colombia	19	34.7	2.4	NS

There is only 1 other sample in which similar reduction in sucker size occurs in several specimens. In a sample from Assateague, Virginia (no. 13), 6 out of 17 males have suckers reduced in diameter in addition to the usual 10-12. However, in the other Assateague sample, reduction occurs in only 1 out of 34; therefore only 7 out of 51 specimens from Assateague samples show increased dorsal reduction of sucker diameter.

Furthermore, 2 specimens from the Caribbean Sea have hectocotylized arms bearing dorsal suckers only 1/2 of the diameter of the ventral suckers from the origin of the hectocotylus to the tip of the arm. Five specimens from the Caribbean have an unusual reduction in the size of a few ventral suckers at the origin of the hectocotylized portion of the arm.

The Caribbean samples appear to have more variation in FW:ML and greater overlap with the FW:ML of *L. plei* than in samples from other areas. However, the analysis of covariance does not show statistically significant differences in these characters between the Caribbean samples of *Loligo pealei* and other samples of *L. pealei.*

A familial character for the family Loliginidae is the presence of 7 buccal lappets. Variation was observed in 12 Caribbean specimens; 164 were examined. One specimen out of 20 examined from the Gulf of Mexico had an abnormal number; none of 132 examined from the east coast of the United States, and 12 of 164 from the Caribbean had an abnormal number. One Louisiana and 3 Colombia specimens have 6 lappets, 8 Colombia specimens have 8, and one Colombia specimen has 9. Nine Colombia specimens were from 1 station (*Pillsbury* 357), where a total of 104 *Loligo pealei* were collected. Lesueur (1821) said that the type specimen from South Carolina had 6 lappets; the type is missing (Voss, 1962).

The margins of the vane of the gladius are usually unthickened although often pigmented. In 6 male *Loligo pealei* of 580 examined, the margin of the vane of the gladius is thickened into a lateral rib equal in thickness to the thickest ribs observed in *L. plei*. These 6 males are: 2 from off North Carolina (223 mm ML, *OREGON II* station 10675; 314 mm ML, *SILVER BAY* station 1219); 1 from off Louisiana (244 mm ML, *OREGON II* station 10858); and 3 from off Colombia (181 mm ML, *CHOCO* station 25; 121 mm, 127 mm ML, *PILLSBURY* station 352). The gladius of the *SILVER BAY* specimen is indistinguishable from that of *L. plei*; it is the only *L. pealei* gladius which I have seen with an index of less than 2.4 for the ratio of vane width to rachis width. The index of 2.1 should identify it as *L. plei*; but its hectocotylus is clearly that of *L. pealei*. This is discussed further in the section on Comparison of Species.

Maturity occurs at a somewhat smaller size in Caribbean specimens than in specimens from other localities. Samples for this study are not random samples of the entire size distribution of each population. The smallest mature males and females respectively found in each sample are: Caribbean 61, 73 mm; Louisiana 138, 133 (however, no smaller specimens are included in the sample), Assateague 86, 87; and Cape Cod 131, 141. The smallest mature Cape Cod specimens were captured in summer. Late fall samples from Cape Cod include immature specimens as large as 190 mm ML (and perhaps 219 mm ML). Summers (1971) believes that large immature autumn squid are representatives of a November brood of the previous year in that region.

Loligo pealei seems to mature at a smaller size in warmer waters. Thompson (1968) states that this is true of many animals and that in addition, animals grow faster at a warmer temperature but reach a smaller maximum size. Embryos of *L. pealei* develop faster at warmer temperatures (McMahon & Summers, 1971). The largest specimens of *L. pealei* are found in the cold part of the range. Summers (1968) recorded a maximum ML of 465 mm. I have seen only one male greater than 200 mm ML and no females larger than 128 mm ML from the warmer waters of the range of *L. pealei*.

According to Summers' (1971) theory, absence of large specimens in the Caribbean could be explained by a longer or year-round breeding season along with death of all *Loligo pealei* after spawning. Death follows spawning in *L. opalescens* (Fields, 1965). Summers believes that the largest males of *L. pealei* are those which missed spawning because they were hatched late in the previous season and were immature or unable to compete successfully for females during the next spawning season. However, as Summers & McMahon (1970) and Summers (1971) said, there is as yet no evidence for breeding mortality. *L. pealei* did not die immediately in studies of spawning in an aquarium (Arnold, 1962). In the currently most successful attempt to keep *L. pealei* alive in an aquarium, 246 squid survived for an average of only 7.4 days (maximum 58 days) and 120 squid survived for an average of 10.3 days. Survival was lower for squid which had reached maturity and for those which bred in captivity (Summers, McMahon & Ruppert, 1974). *L. pealei* observed spawning in nature did not die but left the spawning site after 4 days spent hovering near the eggs (Stevenson, 1934). No mass mortality of *L. pealei* has been described in nature.

Since Gulf and Caribbean squid have been taken in as shallow waters in winter months as in summer, seasonal migrations to deep waters may not occur in the warm part of the range of *Loligo pealei*.

No systematic studies have been made of the distribution and life history of populations of *Loligo pealei* in the Gulf of Mexico and Caribbean Sea. *L. pealei* has been collected at depths of 8-393 m in the Gulf and at depths of 0-73 m in the Caribbean (Table 6, Appendix A). Gravid females were present in samples collected in January from Louisiana and in November from Colombia. Summers (1969) linked seasonal migrations of *L. pealei* to avoidance of winter temperatures below 8°C north of Cape Hatteras. Temperatures as low as 8°C do not occur in the Gulf and Caribbean.

The possibility remains that populations in the warm waters may be adapted to a different critical temperature, but little seasonal variation exists in the surface waters of the Caribbean and surface temperatures remain about 25-28°C. The thermocline at 100-200 m (Gordon, 1966) is below the depth at which *Loligo pealei* has been found to occur. However, Gordon said that upwelling occurs off Colombia and Venezuela; it may expose the populations there to colder water. While summer temperatures in the Gulf of Mexico are tropical, winter temperatures are usually 17-19°C with colder inshore temperatures some years (Leipper, 1954).

Verrill established varieties and subspecies of *Loligo pealei* based upon morphological differences between geographically adjacent populations in New England.

Verrill (1873) described *Loligo pallida* as a distinct species, but in 1881 he reduced it to a variety of *L. pealei* and distinguished it from the typical form of *L. pealei* by its shorter and wider body, broader and larger caudal fin, and larger suckers, especially those of the tentacular club. *L. pealei* var. *pallida* was common in Long Island Sound while the typical form *L. pealei* was common in both Long Island and Vineyard Sound. Considerable overlap exists in the ranges of the ratios Verrill listed for the 2 subspecies.

Verrill (1880) described *Loligo pealei borealis* from off Cape Ann, Massachusetts Bay, but after examining a larger series of specimens he changed it from a subspecies to a geographical variety because he observed specimens showing a gradation between the subspecies and the typical form (Verrill, 1881).

Variation in behavior (presumed to be related to geographic range) was described by Arnold (1962) who observed the establishment of male breeding hierarchies for *Loligo pealei* in an aquarium. Specimens captured in Rhode Island were more aggressive than larger ones from Cape Cod.

I found no evidence of geographical variation in the morphology of samples from New England. Verrill's subspecies are invalid.

LaRoe (1967) reported that there was wide variation in *Loligo pealei*, but little of statistical importance. However, he concluded that 2 large populations of *L. pealei* exist, one in the Caribbean Sea and one from New England waters. Although LaRoe felt that there is clinal variation in some characters between these 2 populations, he suggested that the populations could be 2 allopatric species with ranges meeting at the Yucatan Peninsula, Mexico.

I did not find clinal variation in *Loligo pealei*. Caribbean samples differ only slightly from other geographic samples; they differ little from samples from the Gulf of Mexico. LaRoe's conclusions were based upon smaller samples.

The geographic range of *Loligo pealei* is great, extending from the tropical waters of the Caribbean to the subtemperate waters of Nova Scotia. This represents the largest geographical distribution and greatest range of environmental temperature adaptation of any loliginids in the western North Atlantic. However, no indication of clinal geographic variation exists in the morphology of *L. pealei* although nonmorphological geographic variation remains a possibility and there are small differences in some characters between samples from the Gulf and Caribbean compared with those from farther N.

The species is composed of morphologically variable populations. Whether the variation is phenetic or genetic in origin is not known. The species may be variable as an adaptation to the range of environmental variation it encounters throughout its range, particularly temperature. The nonclinal variation may be brought about through genetic mixing of all populations. This could occur through migrations of adults or movement of planktonic young by currents. *Loligo pealei* is known to migrate seasonally in the northern part of its range, probably in avoidance of temperatures below 8°C. However, large populations have been found in winter as far N as approximately 40° N latitude, so not all members of the species migrate to the Caribbean Sea in winter and there is no evidence that any migrate that distance. How far adults can and do migrate is not known because tagging experiments have thus far been unsuccessful (Summers, 1971, and personal communication). The planktonic young may be carried for considerable distances by currents. The coastal current system of the North American continent is complex, particularly off the eastern coast of the United States (Bumpus & Lauzier, 1965; Gordon, 1966), with many changes throughout the year particularly in the waters close to shore.

The apparently greater variation in Caribbean populations may be related to sympatry with *Loligo plei*; this is discussed later in the comparison of species.

Loligo ocula Cohen, new species

(Figs. 15-20)

MATERIAL: Holotype: ♂, 105 mm ML; *Oregon II* sta. 10858; 22°53′N, 78°43′W; 276 m; 15 Dec., 1969; USNM 727093. Paratypes: 2 ♂ juv., 80, 86 mm ML; *Oregon II* sta. 10858; 22°53′N, 78°43′W; 276 m; 15 Dec., 1969; USNM 727094.—1 ♂, 95 mm ML; 1 ♂ juv., 110 mm ML; 3 ♀ juv., 83-104 mm ML; *Oregon II* sta. 10850; 20°49′N, 73°26′W; 311 m; 13 Dec., 1969; USNM 727098.—1 ♂, 108 mm ML; *Oregon II* sta. 10849; 20°50′N, 73°23′W; 311 m; 13 Dec., 1969; USNM 727097.—1 ♀, 89 mm ML; *Oregon II* sta. 10178; 16°43′N, 81°53′W; 256 m; 16 Nov., 1968; USNM 727096.—2 ♂, 87 mm, 127 mm ML; *Oregon II* sta. 10859; 23°04′N, 78°46′W; 362 m, 15 Dec., 1969; USNM 727095.

DIAGNOSIS: Eye large, diameter of externally visible eyeball about 15-21% of ML (Fig. 19); lens large, diameter of dissected lens about 6-8% of ML (Fig. 20); hectocotylus originating in distal 1/3 to 1/4 of left ventral arm, not extending to arm tip; all modified suckers of dorsal row with broadly triangular bases.

DESCRIPTION: Specimens examined: 80-127 mm ML. *Mantle* cylindrical, tapers posterior to fin insertion to a blunt point. Anterior mantle width rather broad, width 22-29% of ML (Fig. 11); anterior mantle circumference 67-89% of ML; longer specimens more slender. Ventro-lateral lobes on mantle opening short and pointed (point approximately 90° angle); dorsal lobe at least as large as lateral lobes, with rounded point; low, narrow mid-ventral ridge present in males. *Fins* rhomboid, widest point curved and slightly anterior to midpoint of fin length, fins united at posterior end of mantle; width about 45-59% of ML; length 43-54% of ML; width about equal to length, ratio of length to width = 0.783-1.18, fins relatively longer and more narrow in longer specimens; anterior lobes well-developed. *Funnel* well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheetlike. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute and rounded or pointed at tip. Ventral pads oblong, shorter than dorsal pad. Funnel valve broad, bluntly rounded, with thin curved lateral flaps.

Funnel locking-cartilage strong, somewhat long, cartilage length 16-17% of ML (Fig. 21); straight, posterior tip curved dorsally, shallowly grooved. Entire cartilage bordered by thin flange. Mantle locking cartilage straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head large, width about 24-34% of ML (Fig. 22); length about 19-28% of ML; head relatively smaller in longer specimens; nuchal cartilage long (about 18-23% of ML) (Fig. 23), relatively shorter in longer specimens, straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to rounded points; shallow central groove, lateral ridges distinct. Eyes oval, large, diameter of externally visible eyeball 15-21% of ML (Fig. 19), relatively smaller in longer specimens, covered by cornea, pupil round. Lens large, diameter of dissected lens 6-8% of ML (Fig. 20). Dark, sometimes greenish crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order III≥IV≥II>I or III≥II≥IV>I; length of arm I about 20-34% of ML; length of arm II about 29-42% of ML; length of arm III about 35-42% of ML; length of arm IV about 31-40% of ML. Arm III most robust; arms II, IV less robust; arm I least robust, very slender. Swimming keels low, weak, especially on distal 1/2 or 1/3 of arm II; higher, better developed on 2/3 to 3/4 of arm I; best developed on arms III and IV

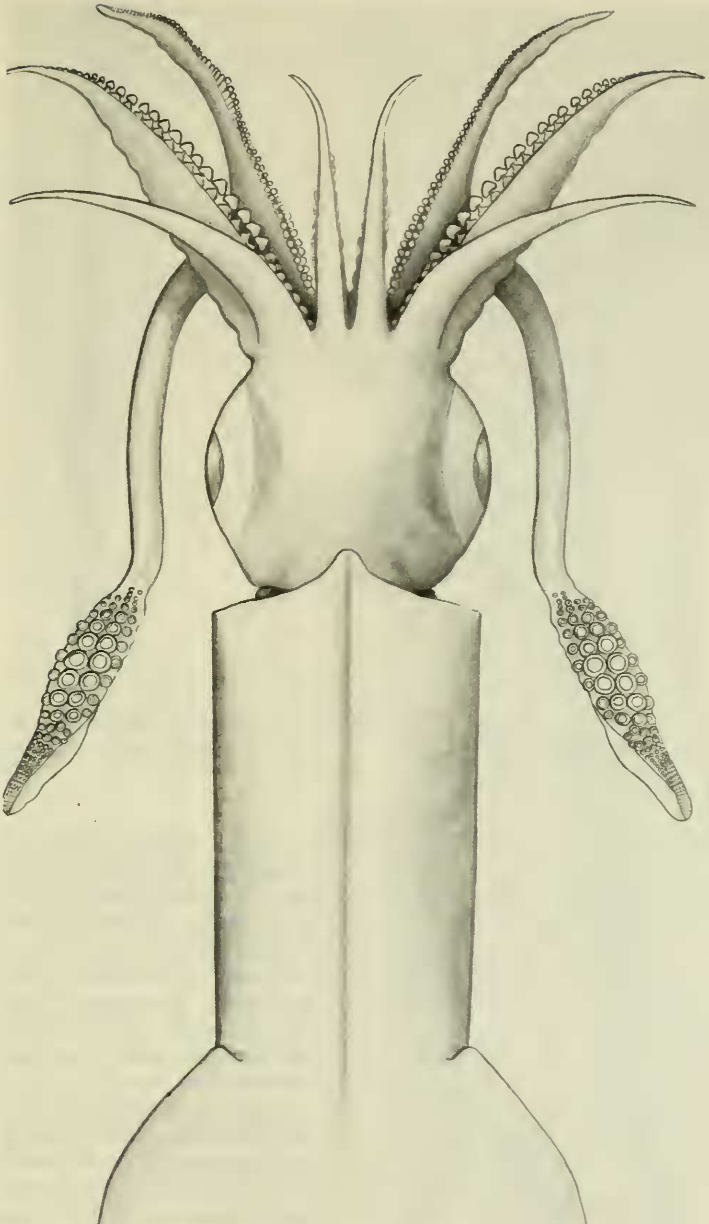

FIG. 15. *Loligo ocula* Cohen, n. sp., holotype; ♂, 105 mm ML, *Oregon II* sta. no. 10858; fins partially drawn from ♀, 104 mm ML, *Oregon II* sta. no. 10850.

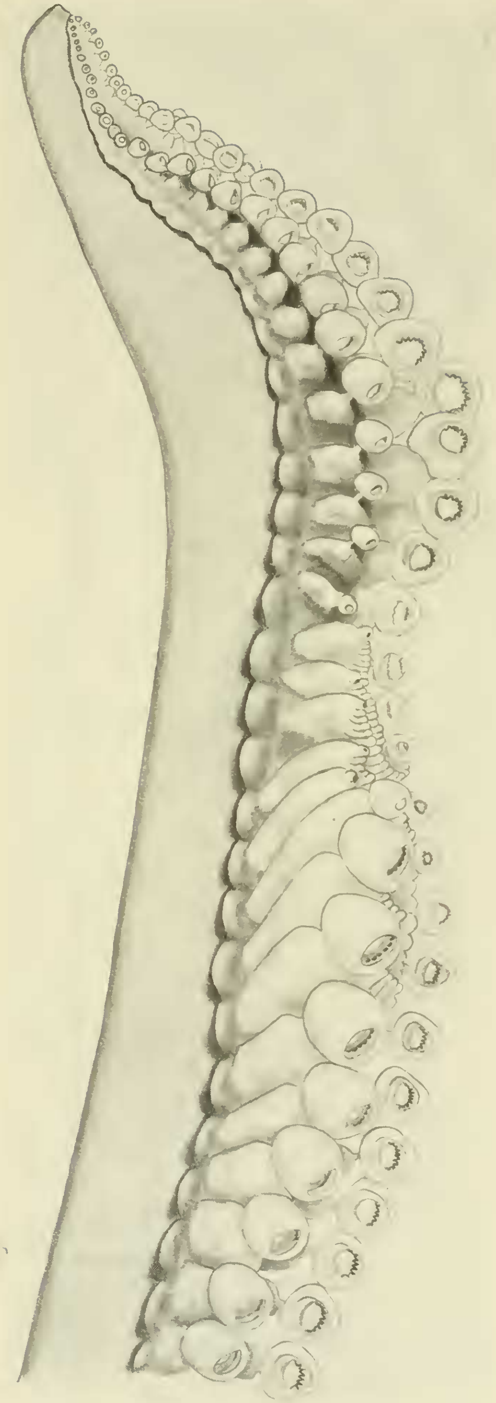

FIG. 16. *Loligo ocula* Cohen, n. sp., hectocotylus; holotype, 105 mm ML; *Oregon II* sta. no. 10858; distal 25 mm (distal 45%) of arm shown.

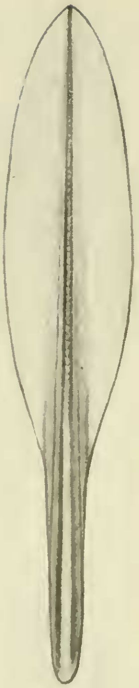

FIG. 17. *Loligo ocula* Cohen, n. sp., gladius; holotype, ♂, gladius length 105 mm, *Oregon II* sta. no. 10858.

where they extend full length of arms; 2 keels on arm IV, dorsal keel of arm IV and keel of arm III arising from same area at base of arms. Protective membranes well-developed, particularly ventral membranes of arms I, II, III; ventral membrane of arm IV least developed; trabeculae long, strong, arise from between bases of sucker stalks, form high points along membranes, less well-developed on arm IV.

Suckers biserial. Number of suckers on arms increases with mantle length; arms I, II, III with about equal numbers of suckers (about 90-100 at 80-95 mm ML, 95-105 at 95-105 mm ML, 105-110 at 127 mm ML); arm IV with about 10 more suckers than other arms. Width of suckers on arms in order III⩾II⩾I⩾IV.

Arm sucker dentition variable (Fig. 18). Teeth present on distal 2/3 of tooth ring. Low, broad, sometimes rippled plate on proximal 1/3 of tooth ring. Arm I with about 7-14 teeth; arm II with about 8-14 teeth; arm III with about 9-11 teeth; arm IV with about 7-8 teeth. Variation in teeth shapes and patterns but arms I, II, and III

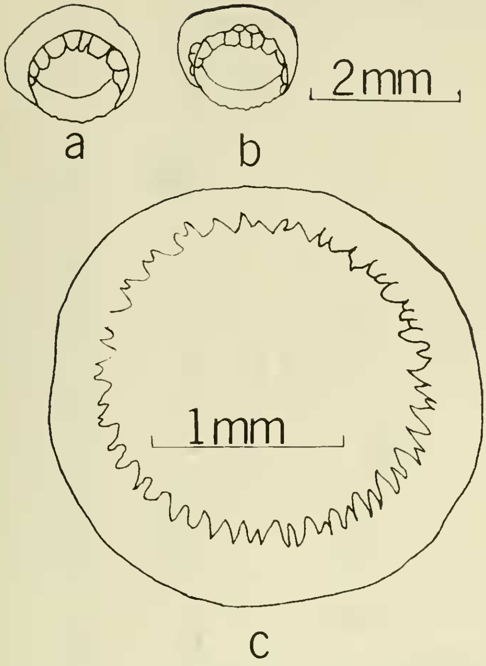

FIG. 18. *Loligo ocula* Cohen, n. sp. **a**, teeth ring of largest sucker on arm III; holotype, ♂, 105 mm ML, *Oregon II* sta. no. 10858; **b**, teeth ring of largest sucker on arm III; other specimen; **c**, teeth ring of large mid-manal sucker on tentacular club; holotype.

often with the following pattern: central 2 teeth of tooth row most narrow, next 2 lateral teeth on either side of central pair increasingly wide; next lateral teeth of decreasing size. Arm IV with irregular patterns but with narrowest teeth near center of tooth row. Tooth shape on all arms varies from very low and blunt in some specimens to longer with blunted points. Smaller tooth rings with relatively narrower teeth.

Left ventral arm *hectocotylized* (Fig. 16), modified in distal 1/3 to 1/4 of arm; modification chiefly in dorsal sucker row, does not extend to tip of arm; only 10-12 suckers in dorsal row less than 1/2 the size of their ventral counterparts. About 33-45 suckers proximal to hectocotylus. Hectocotylization originates proximally with 2-5 suckers of dorsal row larger than their ventral counterparts and on increasingly long, widely triangular pedicels; followed by 5-7 dorsal suckers of rapidly diminishing size on long, large, broadly triangular pedicels of slowly diminishing size distally; ventral suckers in this area diminish in size also but less so and on unmodified pedicels shorter than their dorsal counterparts; ventral suckers at least twice the size of dorsal ones. Suckers of both rows increase in size again distally. Distal tip of arm fairly normal in appearance; suckers of both rows gradually diminish in size; dorsal suckers often slightly smaller than their ventral counterparts. Central area of arm in modified area raised, puffy and folded with central ridge connecting the folded triangular bases of the arms.

Tentacles robust. Clubs expanded, about 24-35% of ML. Clubs with about 32-39 transverse rows of 4 suckers each. Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 2-5 suckers; no carpal knobs. Often only 3 small suckers in proximal-most row of manal suckers; distal rows tetraserial; suckers gradually increase in size; lateral manal suckers smaller than medial suckers; medial manal suckers arise distal to the carpal suckers; about 10-16 medial suckers on manus greatly enlarged; manus terminates rather abruptly, distal-most 1 or 2 rows of manal suckers decrease in size, lateral suckers become more equal in size to medial suckers, ventro-lateral sucker becomes large relative to medial suckers of same transverse row. Dactylus distinct, slender, suckers tetraserial, numerous, minute, decreasing in size distally; suckers in approximately first 10 rows graded in size transversely, ventrolateral sucker largest, dorso-lateral sucker smallest in each transverse row; distal-most 2 transverse rows often triserial and biserial. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of stalk aborally, increases in size on club, particularly on distal 1/3 of manus, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad, heavily supported protective membranes along club, diminish significantly along dactylus. Broad trabeculae between lateral suckers, usually broaden laterally in the shape of a fan, arise from common base of lateral suckers, particularly the distal sucker. Largest suckers on club larger than largest suckers on arm III; ratio of width of largest tentacular sucker to width of largest sucker on arm III = 1.1-2.0.

Club sucker dentition variable (Fig. 18). About 24-30 teeth, usually 24, on sucker rings of carpal area; teeth usually bluntly

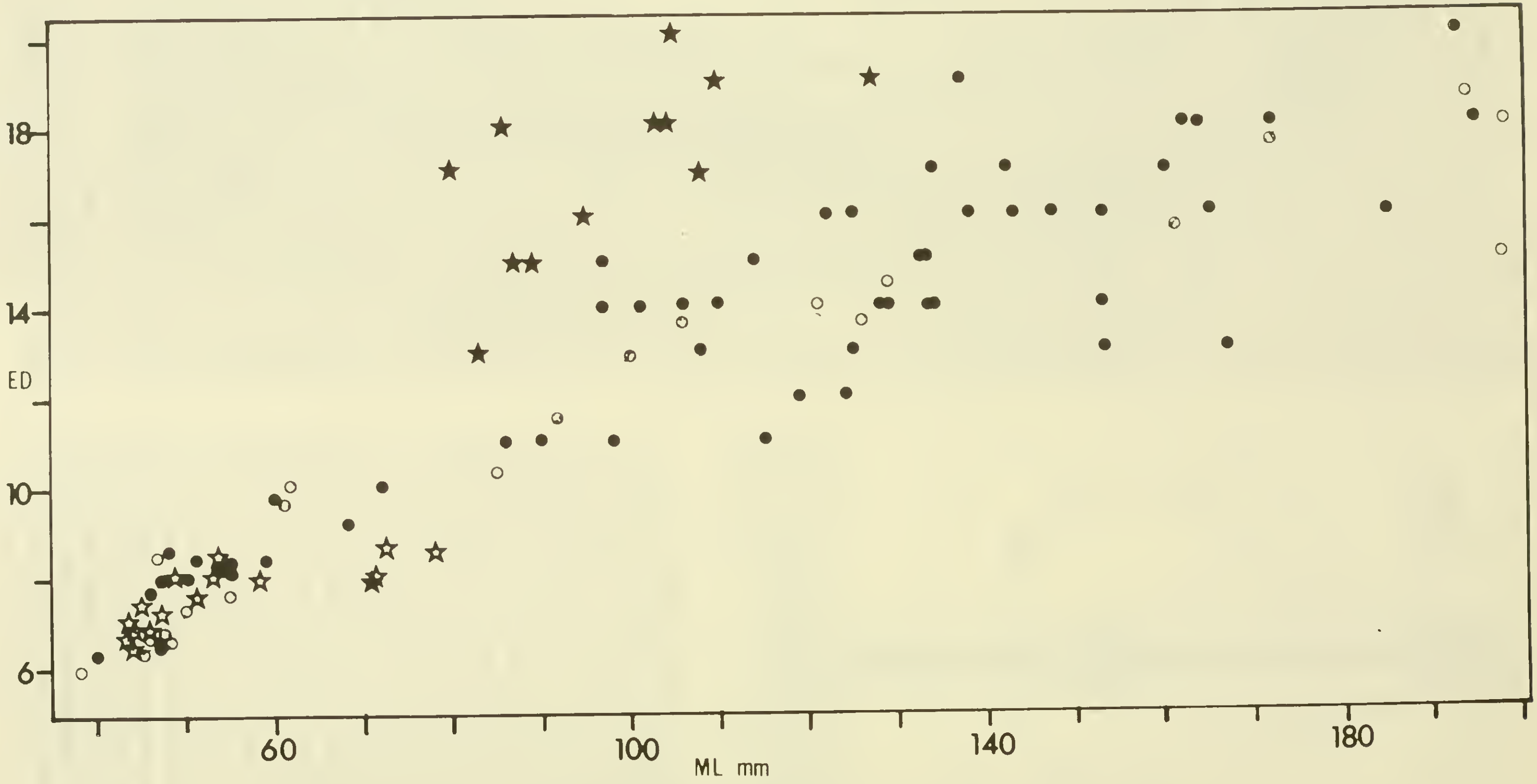

FIG. 19. The regression of diameter of externally visible eyeball upon mantle length (ED:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars.

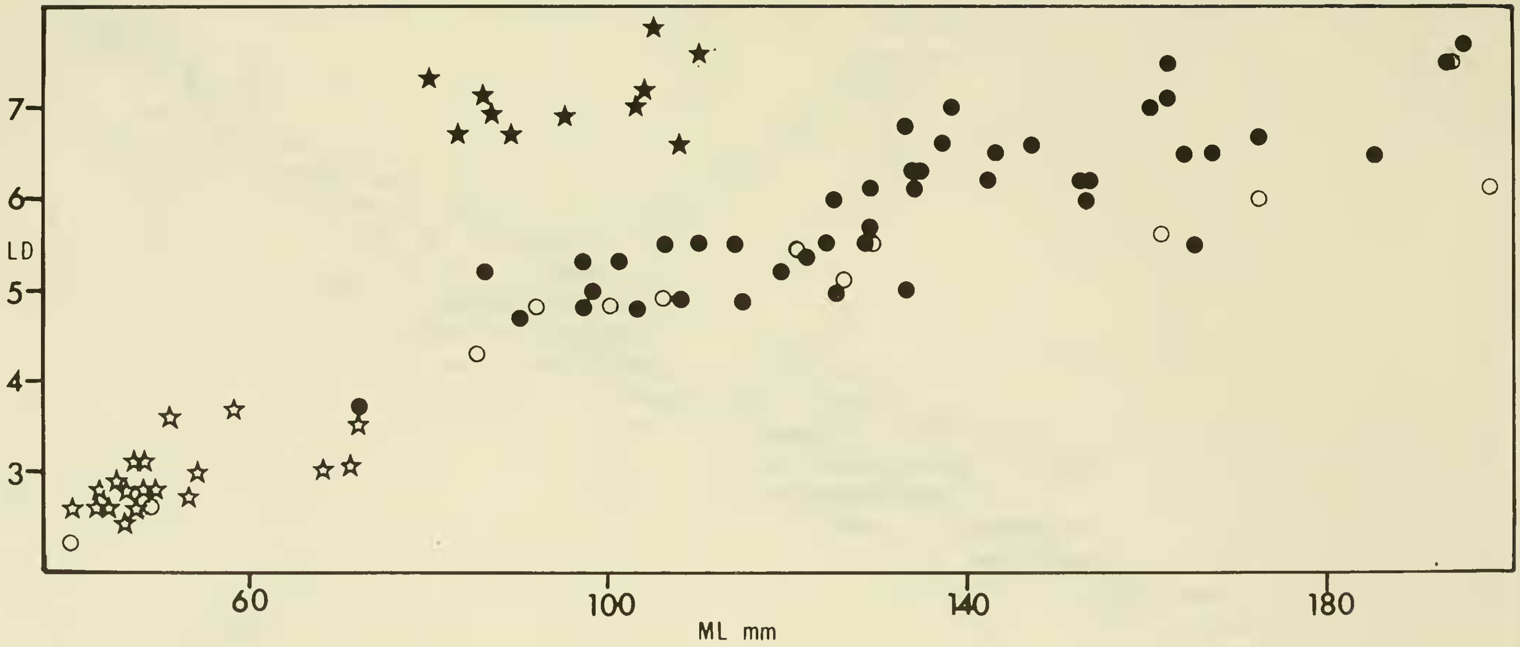

FIG. 20. The regression of diameter of dissected lens of eye upon mantle length (LD:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars.

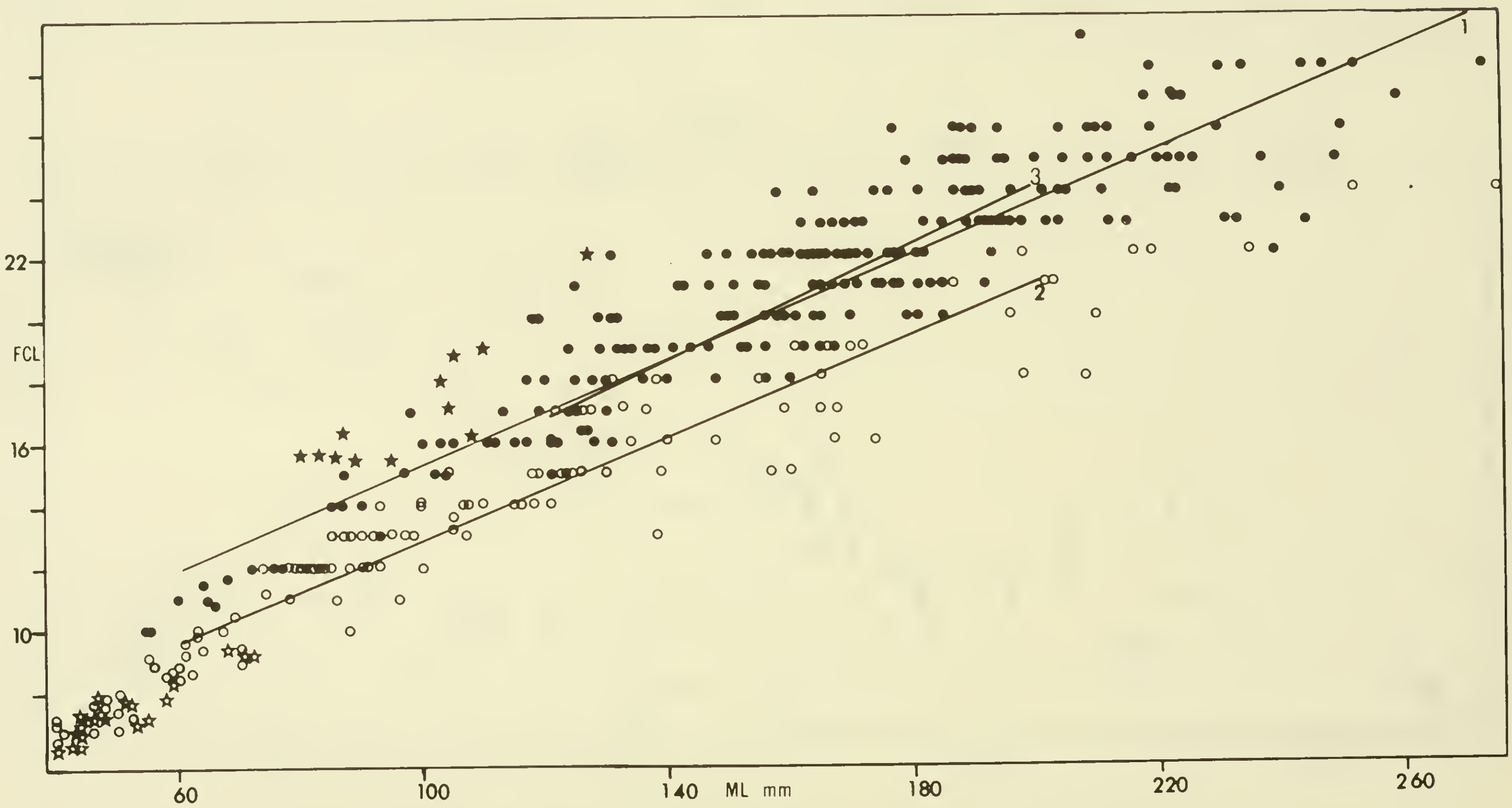

FIG. 21. The regression of funnel cartilage length upon mantle length (FCL:ML). *Loligo pealei* = solid circles, regressions nos. 1, 3 (120-200 mm ML only); *L. plei* = open circles, regression no. 2. *L. ocula* = solid stars. *L. roperi* = open stars.

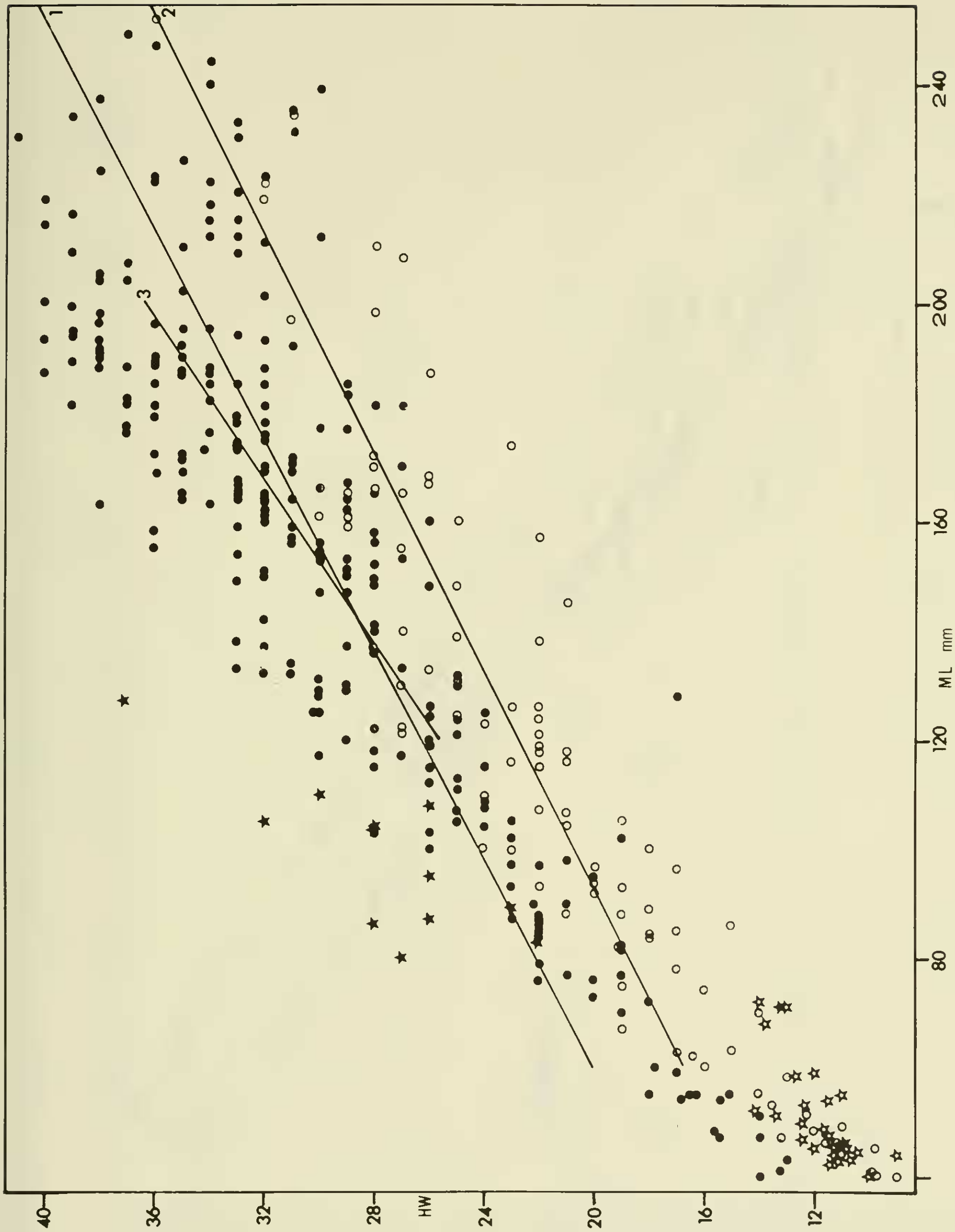

FIG. 22. The regression of head width upon mantle length (HW:ML). *Loligo pealei* = solid circles, regressions nos. 1, 3 (120-200 mm ML only). *L. plei* = open circles, regression no. 2. *L. ocula* = solid stars. *L. roperi* = open stars.

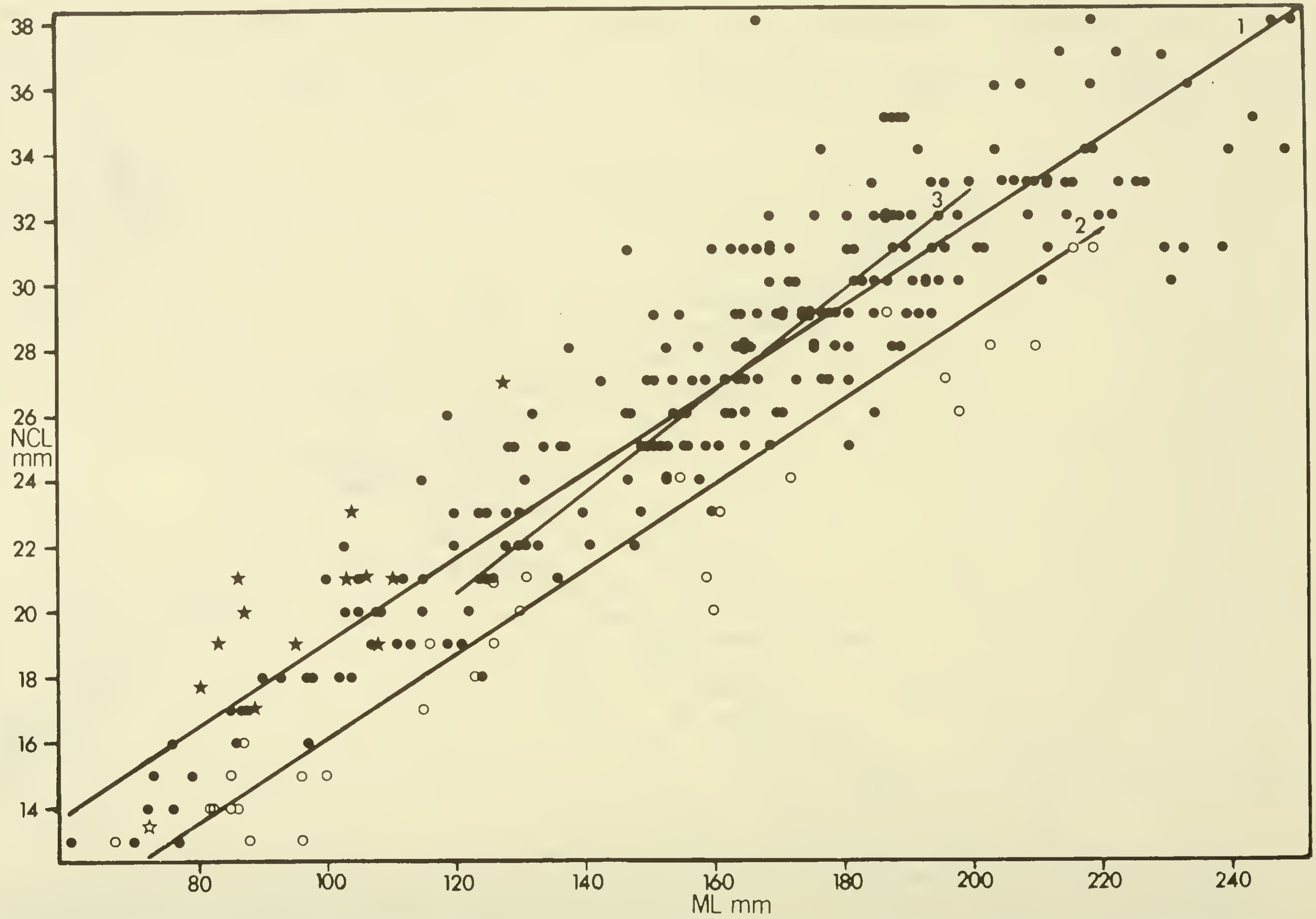

FIG. 23. The regression of nuchal cartilage length upon mantle length (NCL:ML). *Loligo pealei* = solid circles, regressions nos. 1, 3 (120-200 mm ML only). *L. plei* = open circles, regression no. 2. *L. ocula* = solid stars. *L. roperi* = open stars.

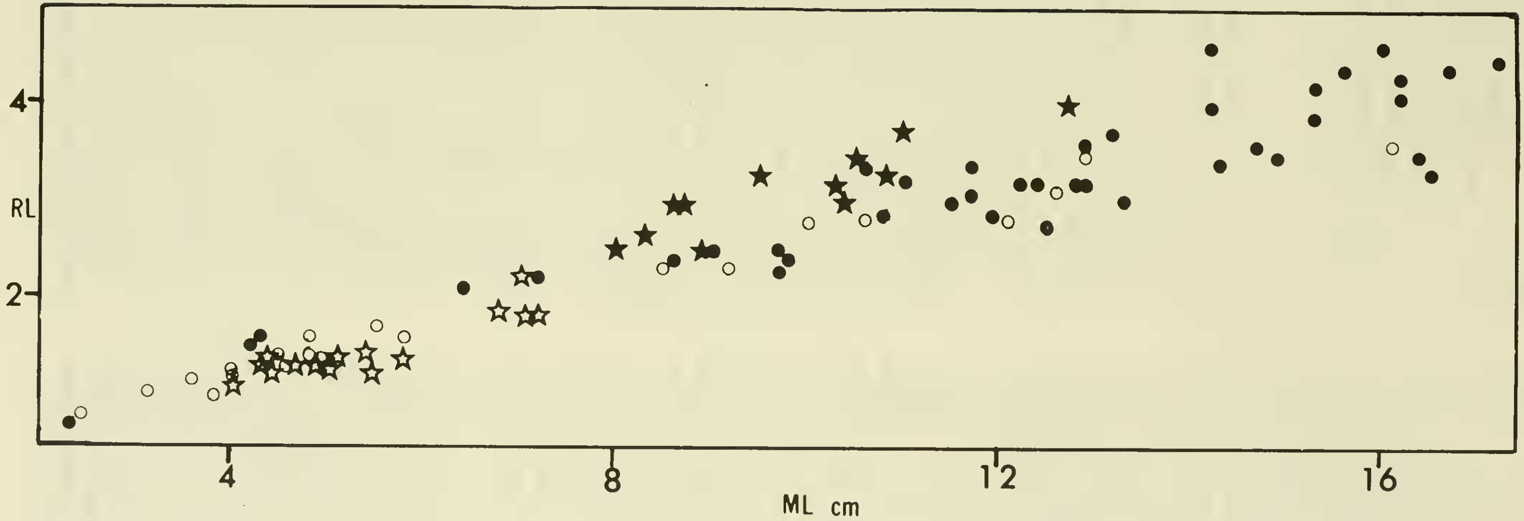

FIG. 24. The regression of rachis length upon mantle length (RL:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars.

pointed, varying from blunt to pointed; teeth graded in size, proximal teeth larger, usually more pointed than distal teeth. About 15-27 teeth on proximal-most lateral suckers; about 23-35 teeth on largest lateral suckers; about 15-25 teeth on distal lateral suckers; teeth usually pointed, points often curved, sometimes bluntly rounded instead of pointed; teeth graded in size, and sometimes alternating large and small; teeth at outer edge of ring larger and usually more pointed than inner teeth. About 22-28 teeth on proximal-most medial manal suckers (first 1-3); about 35-60 teeth on largest medial manal suckers; about 22 teeth on distal medial manal suckers; teeth usually pointed, usually triangular in shape, points sometimes slightly curved, sometimes bluntly rounded, often with alternating large and small teeth (a pattern of large tooth, small tooth, medium-sized tooth, small to medium-sized tooth, medium tooth, large tooth and a pattern of large, small, small, large each observed once). About 20 usually pointed (sometimes stubby and rounded) teeth on proximal dactylar sucker rings; about 8 teeth larger and usually more pointed than others.

Gladius (Fig. 17) long, rather wide (width about 13-17% of ML), feathershaped; anterior tip with weak flexible acute point; rachis stiff, free rachis long, about 28-35% of ML (Fig. 24); median ridge and heavy lateral rods on rachis, continue in center of vane, fuse beyond midpoint of vane, continue to tip. Vane tapers at both ends from widest point in central area, edges thin, posterior tip pointed and thin. Rachis rather narrow, vane rather wide; ratio of greatest width of vane to greatest width of rachis about 2.4-2.9.

Buccal lappets usually 7 (8 in holotype: left dorsal lappet doubled); ventral pair united at base and with fewer suckers; suckers present on all lappets; total suckers on all lappets 45-64. Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I-IV respectively.

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella), heavily pigmented; dorsal hood weak, thin, lightly pigmented; notch separates rostrum and rostral lamella (jaw angle recessed); cutting edge of rostral lamella slightly curved, smooth, small convex curve adjacent to rostrum; palatine lamella weak, large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge curved; rostral lamellae narrow, short, with wing lobate, thin; gular lamella large, crest strong, posterior corner pointed, moderately curved.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth and pointed lateral cusps; 1st lateral tooth pointed, with pointed lateral cusp; 2nd lateral tooth pointed, curved on outer side, longer than first, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 70-80% of total length, cement body about 7-13% of total length, total length about 6-14 mm. Cone at oral end of cement body cylindrical, narrows at oral end.

Gill length about 26-35% of ML. Number of filaments on one side of gill increases with ML, about 53-56 at 80-90 mm ML, 61-65 at 95-127 mm ML.

Color (in alcohol). Reddish-brown chromatophores cover entire mantle, more widely spaced ventrally; present only on dorsal side of fins and more widely-spaced laterally; cover entire head, more closely-spaced proximal to eyes; present on exposed part of funnel and collar; present on outer side of arms and tentacles. Dark, sometimes greenish crescent over dorsal border of eyes. Dark mid-dorsal longitudinal indentation extends from mid-dorsal mantle point to just posterior of fin origin, more than 1/2 of ML.

HOLOTYPE: United States National Museum (727093). Paratypes: United States National Museum (727094, 727095, 727096, 727097, 727098).

TYPE LOCALITY: 22°53′ N; 78°43′ W on edge of Grand Bahama Bank about 45 mi N of Punta Alegre, Cuba; *Oregon II* station 10858, 15 December 1969, 276 m.

DISTRIBUTION: Caribbean Sea: between Cuba and Great Bahama Bank; S of Great Inagua Id., Bahama Ids.; off continental shelf, E of Honduras (Fig. 1). Taken in bottom trawls at depths of 256-362 m. This species has been caught together with *Loligo roperi* (Table 3).

ETYMOLOGY: The Latin word "*oculus*" means eye, and refers to the large, prominent eyes of *L. ocula.*

DISCUSSION: The holotype of *Loligo ocula* has 8 buccal lappets (all of the others have 7). While 7 buccal lappets is a familial character for the Loliginidae, aberrations in the number of lappets occur as noted here in *L. plei* and in *L. pealei* (including its holotype).

Fig. 6 indicates that females may have fewer gill filaments than males. However more specimens are necessary to verify that this is as true of *Loligo ocula* as it is of *L. pealei*.

Loligo plei Blainville, 1823
(Figs. 25-26)

Loligo pleii Blainville, 1823: 132-133.——Férussac & d'Orbigny, 1834-48, pl. 16.

(?)*Loligo brasiliensis* Blainville, 1823.——Férussac & d'Orbigny, 1834-48: 313-314.

Loligo plei Blainville.——Férussac & d'Orbigny, 1834-48: 312-313.——d'Orbigny, 1853: 42-45.

Doryteuthis plei (Blainville).——Naef, 1912: 742.——Adam, 1937: 63-67, figs. 18-22; 1941: 132-133.——Rees, 1950: 111-113, pl. 14.——Voss, 1956: 116-118, fig. 6, b-d.

DIAGNOSIS: Ratio of greatest width of vane of gladius to greatest width of free rachis 1.5-2.4, vane of mature males with thickened rod-like margins; hectocotylus originating in distal 1/4 to nearly 1/2 (not more than 50%) of left ventral arm, extending to arm tip, at least 1/2 (but less than 70%) of the suckers in the dorsal row less than 1/2 the size of their ventral counterparts.

DESCRIPTION: *Mantle* long, slender, cylindrical, tapering to a posterior acute point. Anterior mantle width about 11-25% of ML (49-348 mm ML); anterior mantle circumference 35-68% of ML (44-348 mm ML), longer specimens more slender. Ventro-lateral lobes on mantle opening short and pointed (point approximately 90° angle); dorsal lobe longer than lateral lobes, with rounded point; low, narrow, mid-ventral ridge often present, particularly on males.

Fins rhomboid, sides fairly straight, widest point curved and slightly anterior of midpoint of fin length; fins united posterior to tip of mantle; length (35-58% of ML, 40-348 mm ML) about equal to width (33-45% of ML, 40-348 mm ML), fins relatively longer and more narrow in long specimens, ratio of length to width is about 0.765-1.66; anterior lobes well-developed.

Funnel well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheet-like. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute, very inconspicuous, pointed. Ventral pads oblong, shorter than dorsal pad. Funnel valve broad, shallowly curved or blunt with thin curved lateral flaps.

Funnel locking-cartilage long (about 7-18% of ML, 60-348 mm ML), straight, posterior end slightly wider and curved dorsally, shallowly grooved. Mantle locking-cartilage straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head width about 10-41% of ML, length about 10-22% of ML (44-348 mm ML), head relatively smaller in large specimens; nuchal cartilage long (about 11-19% of ML, 44-348 mm ML), relatively shorter in long specimens, straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to blunt or rounded points; shallow central groove, lateral ridges distinct. Eyes oval, covered by cornea, pupil round. Diameter of externally visible eyeball about 14-19% of ML (40-319 mm ML), diameter of dissected lens about 2-7% of ML (40-348 mm ML). Dark crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order III≥IV≥II>I or III>II≥IV>I; length of arm I about 16-26% of ML; length of arm II about 23-31% of ML; length of arm III about 25-37% of ML; length of arm IV about 21-32% of ML (44-348 mm ML). Arm III robust, arms IV, II less robust, arm I least robust, very slender. Swimming keels 3rd best developed on arm I, flaring before midpoint, decrease to very low distally; very low and weak on arm II, decrease distally, best-developed on arm III, flared before midpoint, decrease gradually distally; 2nd-best developed on arm IV, 2 keels decrease gradually distally, dorsal keel better developed; dorsal keel of arm IV and keel of arm III arise from same area at base of arms. Protective membranes well-developed, particularly ventral membranes on arms I, II, III; poorly developed, particularly dorsal membrane on arm IV; trabeculae long, strong, except on arm IV, arise from base of

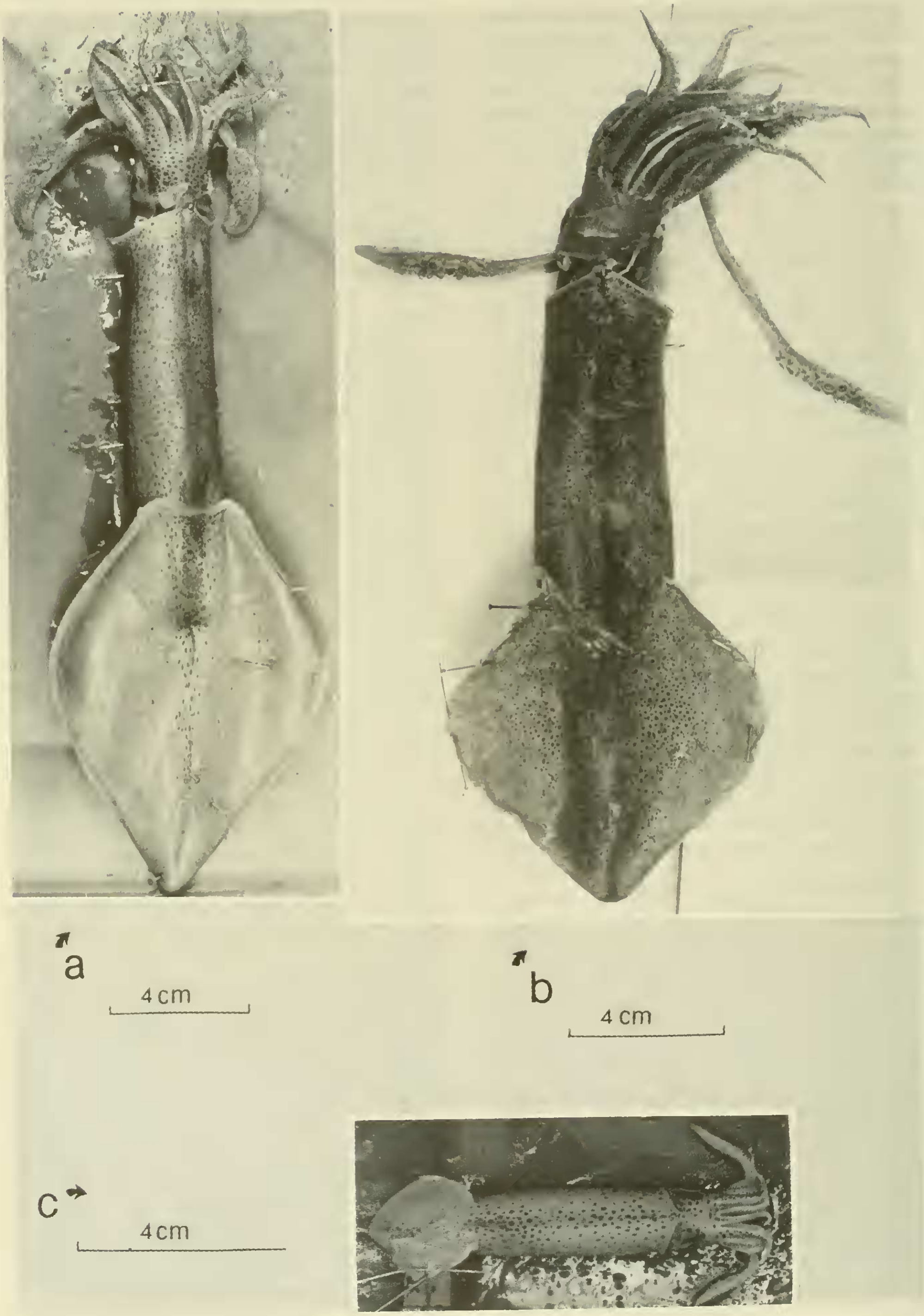

FIG. 25. *Loligo plei.* **a**, ♂, 200 mm ML; Oregon sta. no. 6777; **b**, ♀, 161 mm ML, *H. Cortez*, FSBC no. 12131; **c**, ♀ juv., 69 mm ML, *Geronimo*, cr. 6, no. 8.

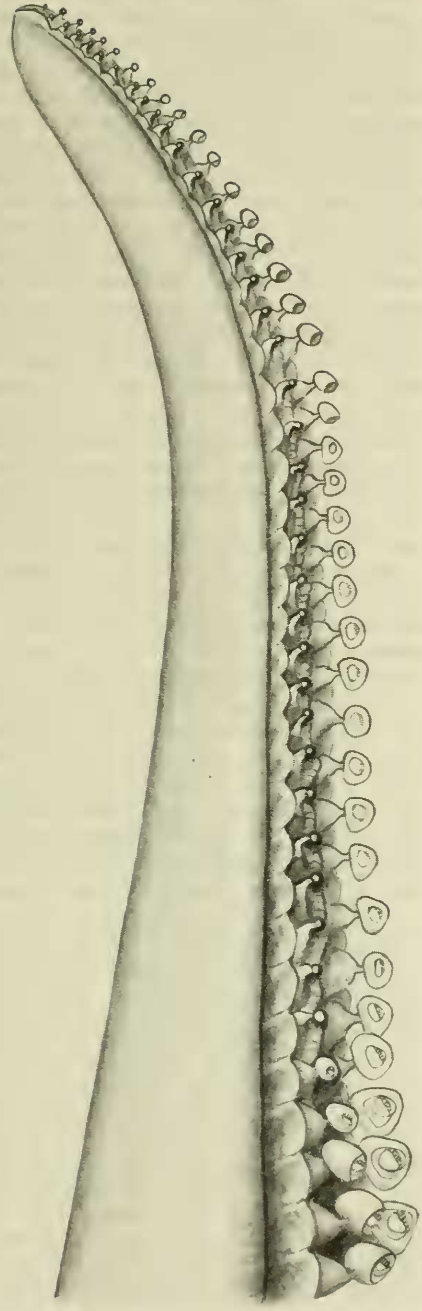

FIG. 26. *Loligo plei* Blainville; hectocotylus; ♂, 194 mm ML; *Choco* sta. no. 50; distal 34 mm (distal half) of left ventral arm.

sucker stalks, form high points along membranes. Suckers biserial. About 5 to 15 proximal-most suckers on arms I, II, III, sometimes IV increase in size distally, followed by gradual decrease in size of suckers; rapid decrease in size of suckers on arm III following about 20-34th sucker. Number of suckers on arms increases with mantle length; about 50-120 suckers on arm I, about 70-120 on arms II, III, about 90-130 on arm IV (40-348 mm ML). Width of suckers on arms in order III≥II≥I≥IV.

Arm sucker dentition variable. Teeth present on distal 1/2 of tooth ring (absent rarely, apparently worn down). Low, narrow plate on proximal 1/2 of tooth ring. About 5-10 teeth on each arm. Teeth shapes and patterns vary; tips of teeth usually blunt or rounded; teeth sometimes square, center 1-4 teeth often narrowest, lateral teeth decrease in size, pattern not always symmetrical. Some or all teeth very pointed on some or all suckers of right ventral arm (IV) of some males; teeth usually blunt on proximal-most suckers.

Not more than 1/2 of left ventral arm *hectocotylized* (about 26-50%; 38-348 mm ML) (Fig. 26). Modification usually in dorsal sucker row only, extends to arm tip. About 4-8 proximal-most suckers in dorsal row increase slightly in size distally, followed by about 5-12 decreasing slightly in size distally; followed by hectocotylized suckers rapidly diminishing in size of suckers while increasing in height of pedicels; all succeeding suckers in dorsal row with minute suckers (much less than 1/2 the size of their ventral counterparts), on small, narrow triangular pedicels (only about 3-4 proximal-most modified suckers on enlarged pedicels); about 42-82 suckers (dorsal and ventral rows) distal to origin of hectocotylus (about 52-69% of total suckers on arm; 38-348 mm ML). Central area of arm with low folds and low ridge in hectocotylized area.

Tentacles robust. Clubs expanded, about 19-29% of ML (44-348 mm ML). Clubs with 27-38 transverse rows of 4 suckers each (31-348 mm ML). Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 1-4 suckers; no carpal knobs. Often only 3 small suckers in proximal-most row of manus; distal rows tetraserial, suckers gradually increase in size; about 10-14 medial suckers on manus greatly enlarged; lateral manal suckers smaller than medial suckers; manus terminates rather abruptly; distal-most 1 or 2 transverse rows of manal suckers decrease in size, ventro-lateral sucker usually larger than dorso-lateral sucker in distal row of manus and for as many as 14 rows of dactylus. Dactylus distinct, slender, suckers tetraserial, numerous, minute, decreasing in size distally; distal-most 2 transverse rows often triserial and biserial. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of stalk aborally, increases in size on manal region of club, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad heavily supported protective membranes along club, diminish significantly along dactylus particularly on dorsal side. Broad trabeculae between lateral suckers, usually broaden laterally in the shape of a fan, arise from common base of lateral suckers particularly the distal sucker, slight contribution from proximal sucker also in many larger specimens. Width of largest sucker greater than width of largest sucker on arm III (ratio of width of largest sucker of tentacle to width of largest sucker on arm III: 1.29 to 2.09).

Club sucker dentition variable. Sucker rings of carpal area with about 10-30 teeth (rarely none), varying from blunt to pointed, graded in size, teeth on 1/2 of ring very small, sometimes only a rippled edge, about 5-12 large teeth. Teeth of lateral manal suckers usually pointed, teeth graded in size, sometimes large and small teeth alternate, teeth at outer edge of ring larger and usually more pointed than inner teeth; largest lateral suckers with about 17-25 teeth. Teeth of medial manal suckers usually pointed, usually triangular in shape, points sometimes slightly curved, sometimes rounded, teeth rarely worn down to rounded stubs; patterns of teeth arrangement vary, teeth often arranged in a pattern of alternating large and small teeth, occasionally almost equal in size, very rarely teeth arranged in trinary pattern described in *Loligo pealei*; largest medial manal suckers with about 26 to 46 teeth. Proximal dactylar sucker rings with about 15 to 20 teeth, usually pointed, sometimes blunt or rounded stubs, graded in size, about 5 to 10 teeth larger than rest (specimens examined: 92-319 mm ML).

Gladius long, slender (width about 7-22% of ML, 40-348 mm ML), feather-shaped; anterior tip with weak flexible acute point; rachis stiff, free rachis length about 18-33% of ML (40-280 mm ML); median ridge and strong, thick lateral rods on rachis continue in center of vane, fuse beyond midpoint of vane, extend length of gladius. Additional lateral rods usually border most of vane, strongest in large mature males, weakest, sometimes rather indistinct (only a thickened stripe) in immature females, posterior portion often only a colored stripe. Rachis rather wide, vane rather narrow; ratio of greatest width of vane to greatest width of rachis about 1.5-2.4 (38-348 mm ML). Vane tapered at both ends, greatest width in males usually near anterior shoulders of vane, greatest width in females near center of vane, sides of vane fairly straight (curved in many females). Posterior tip pointed and thin.

Buccal lappets usually 7 (rarely 5 or 6), 7 buccal connectives, 7 supporting rods. Suckers (maximum 16) present on each lappet, total suckers on all lappets about 16-66, rarely fewer (suckers may have fallen off). Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I to IV respectively (specimens examined 44-348 mm ML).

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella), heavily pigmented; dorsal hood weak, thin, lightly pigmented, notch separates rostrum and rostral lamella (jaw angle recessed); cutting edge of rostral lamella slightly curved, smooth, small convex curve sometimes adjacent to rostrum; palatine lamella weak, large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge slightly curved, jaw angle obtuse but nearly 90°; rostral lamellae narrow, short, wing lobate, thin; gular lamella large, crest strong, posterior corner pointed, moderately curved.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth and pointed lateral cusps; 1st lateral tooth pointed and with pointed lateral cusp; 2nd lateral tooth pointed, longer than 1st, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 51-77% of total length, cement body about 8-15% of total length; total length about 4-13 mm (62-280 mm ML). Oral connection of cement body cylindrical, narrows at oral end.

Gill length about 20-32% of ML (44-348 mm ML). Number of filaments on gills increases with ML, number of filaments on one side of gill 53-84 (44-348 mm ML).

Color (in alcohol). Reddish-brown chromatophores present on entire mantle, larger and more closely-spaced on dorsal side, particularly in mid-dorsal region, often arranged in longitudinal stripes on anterior ventral-lateral mantle of large, mature males; present only on dorsal side of fins; cover entire head, more closely-spaced dorsally, particularly proximal to eyes; present on collar and funnel, on outer sides of arms, tentacles, trabeculae and protective membranes of arms I, II, III, and tentacles. Dark crescent over each dorsal border of eye. Mid-rib of gladius visible externally as an anterior reddish-brown, mid-dorsal indentation.

HOLOTYPE: Muséum National d'Histoire Naturelle, Paris.[3]

TYPE LOCALITY: Martinique, Lesser Antilles.

DISTRIBUTION: Continental shelf and slope of the E coast of the North and South American continents from Cape Hatteras (very rarely Rhode Island) to Fortaleza, Brazil (LaRoe, 1967); Bermuda; islands of the Bahamas and the Caribbean Sea (Fig. 1). Taken by dip net at the surface; in bottom trawls at depths of 3-366 m.

DISCUSSION:

Nomenclature: *Loligo pleii* is the original spelling by Blainville (1823), but *L. plei* is the commonly used spelling and the species was actually named after a Monsieur Plée. Pending a decision on the request to the Commission by Smith, Stuart & Conant (1971), I will use *plei*.

Geographic Distribution: Four *Loligo plei* were caught off Newport, Rhode Island, in 1880: a mature male, 84 mm ML, and 2 immature females, 63 and 93 mm ML (USNM no. 51271, *FISH HAWK* sta. no. 800, 16 August, 1880); and a mature male, 107 mm ML (USNM no. 33189). I know of no other *L. plei* caught N of Cape Hatteras. The temperatures for *FISH HAWK* no. 800 were: bottom and surface 20°C. Station records for 1874-1887 of the *FISH HAWK*, *SPEEDWELL*, and *BLUELIGHT* indicate that these temperatures are not unusual in August. However, these squid must represent rare northern strays. A similar rare northern record for the tropical species *Sepioteuthis sepioidea* at Woods Hole, Mass. in July, 1938, is reported by Mercer (1970b) who suggested that it was carried northward by the Gulf Stream.

Loligo plei has been caught in the same bottom trawls as *L. pealei* and *L. roperi*, with *L. pealei* alone, and with *Lolliguncula brevis* (Table 3).

Sexual dimorphism: Some sexual dimorphism is obvious in *Loligo plei*. The vane of the gladius is wider in females (11-22% of ML, 42-203 mm ML) than in males (7-11% of ML, 40-348 mm ML) (Fig. 5). The vane of female gladii usually has curved, tapered margins with weak lateral ribs; the widest point is near the center of the vane. Male gladii usually have straighter margins with stronger lateral ribs; the widest point is anterior to the midpoint. Ventral longitudinal ridges on the mantle are more often present in males than in females. Mature males often have ventro-lateral stripes of chromatophores. The sexes of *L. plei*, unlike those of *L. pealei*, do not appear to differ in gill length or number of gill filaments (Fig. 6). Statistical analysis of sexual dimorphism was not made.

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[3] Since the text was completed I have had the opportunity to visit the Muséum national d'Histoire Naturelle in Paris, where I examined a specimen which is probably the holotype designated by Blainville. This specimen is a mature male *L. plei*, 156 mm ML, collected by M. Plée in Martinique. Unfortunately the specimen does not bear a label that specifies it as the type. Blainville (1823: 132-133) gave a short, 119 word description of *L. plei*; he did not list the measurements or illustrate his specimen. However Blainville stated that his specimen was sent to him from the seas of Martinique by M. Plée and that it was kept in the collection of the Muséum national d'Histoire Naturelle. The specimen which I examined agrees with Blainville's description. In particular it has no teeth on the sucker rings of the arms nor on the largest mid-manal tentacular suckers. This is very unusual in *L. plei*; I have seen only 1 other specimen which lacked teeth. This may be an artifact of preservation or a natural wearing of the teeth. Blainville stated that the chitinous ring of the suckers of his specimen was whole or entire; I believe that he meant that it was smooth or lacked teeth.

I cannot be absolutely certain that this is Blainville's original specimen because occasionally in the past, original specimens may have been replaced by more attractive specimens. However this specimen fits the brief original description. It is a mature male, and though old, it is in fairly good condition. Therefore I must assume that this specimen is indeed the holotype of *L. plei*.

Counts and measurements are as follows: ML 156 mm; FL 76 mm; FW 49 mm; AMW 21 mm; FCL 15 mm; NCL 21 mm; HL 18 mm; ED 10 mm; AL I 30 mm; AL II 35 mm; AL III 38 mm; AL IV 36 mm; the hectocotylus is 11 mm in length and extends to the tip of the left ventral arm which is 34 mm in length; the hectocotylized arm bears 86 suckers of which about 48 suckers are present in the hectocotylized area; about 33 transverse rows of suckers on the tentacle club; no teeth on largest mid-manal suckers; broadly triangular, widely-spaced, pointed teeth on smaller proximal mid-manal suckers; mid-manal suckers about twice the size of lateral manal suckers; RL 31 mm; RW 7 mm; GW 12 mm; lateral edge of vane of gladius thickly ribbed; suckers present on all buccal lappets.

Maturity: LaRoe (1967) found gravid *Loligo plei* during all months but June and August. *L. plei*, unlike many other squid may not die after spawning but continue to grow and spawn again. Roper (1965) described spawning in an aquarium by one *L. plei*; it spawned a 2nd time after 4 days and remained healthy for nearly a week. Waller & Wicklund (1968) observed spawning underwater and saw no mortality. Spermatophores are present in males ranging in size from 38 mm ML (*GILL* cruise 4, sta. no. 19, off eastern Florida) to 348 mm ML (*CHOCO* sta. no. 11, off Colombia, 3 May, 1969); eggs are present in females ranging in size from 42 mm ML (USNM no. 575445, off Georgia, 1957) to 203 mm ML (*CHOCO* sta. no. 11, off Colombia). Apparently immature males and females as large as 139 mm ML (USNM no. 577080, off Puerto Rico, 26 Oct., 1966) and 90 mm ML (USNM no. 574327, off Georgia) respectively were observed.

Surprisingly, single trawl hauls have caught small mature *Loligo plei* along with much larger immature ones. Immature *L. plei* 52-91 mm ML (hectocotylus not fully developed) were caught with a mature male *L. plei*, 55 mm ML (spermatophores present, hectocotylus developed) off South Carolina in June (USNM no. 575408). Immature *L. plei* 80-138 mm ML were caught with mature *L. plei* 52-61 mm ML off Georgia (USNM no. 574327). Many immature *L. plei* 37-91 mm ML were caught with 3 mature *L. plei* 48-78 mm ML off North Carolina in October (*DELAWARE II* sta. no. 10). I could find no morphological differences between mature and immature specimens; I believe they belong to the same species. Why did the squid of the same area not mature at the same time? Since these were open nets some specimens may have been caught while the net was being retrieved. The mature and immature squid may have originated in different waters of different temperatures and somehow come together later on. I will discuss possible implications for speciation later in comparing *L. plei* with *L. roperi*.

Geographic variation: A familial character for the family Loliginidae is the presence of 7 buccal lappets. Some variation was observed in *Loligo plei* as well as in *L. pealei* and *L. ocula*. Four specimens of *L. plei* have missing buccal lappets; 155 specimens were examined. A 166 mm female caught off North Carolina (*SILVER BAY* sta. no. 1222) has 6 lappets. Three of the 10 specimens from Bermuda have missing lappets. These 3 specimens lack the 3rd, the 4th, and the 4th and 5th lappets respectively. The unusual percentage of abnormalities in the number of buccal lappets could be due to the isolation of what is probably a small population of *L. plei* at Bermuda. *L. plei* probably was introduced to Bermuda from the S (Voss, 1960). It is likely that it arrived from the West Indies via the Gulf Stream as have many shore fishes (Collette, 1962) and invertebrates (Ekman, 1953). Collette (1962) noted character differences between mainland stocks of shore fishes and their endemic derivatives or populations at Bermuda which could be correlated with scarcity of food in the Sargasso Sea around Bermuda. Collette also found that endemism is less than 4% in shore fishes—probably because of continued influx of individuals via the Gulf Stream. *L. plei* of Bermuda do not differ in most respects from the populations of other localities, and planktonic young and nektonic adults may be reintroduced to Bermuda frequently.

Loligo roperi Cohen, new species

(Figs. 27-30)

MATERIAL: Holotype: ♂, 70.8 mm ML; *Geronimo* sta. 8-26; 25°42.5′N, 79°20′W, off Bimini, Bahama Ids.; night light; 6 June, 1966; USNM 727777. Paratypes: 2 ♂, 67.9, 70.5 mm ML; *Geronimo* sta. 8-26; 25° 42.5′N, 79°20′W; off Bimini, Bahama Ids.; night light; 6 June, 1966; USNM 727776.—3 ♂, 16 ♀, 44.3-58 mm ML; *Oregon II* sta. 187; 14°49′N, 81°39′W; 48 m; 19 Nov. 1968; USNM 727775.—1 ♀, 72 mm ML; *Oregon II* sta. 10858; 22°59′N, 78°43′W; 278 m; 15 Dec. 1969; USNM 727774.—3 ♂, 2 ♀, 44-58 mm ML; *Choco* sta. 6902-38; 9°3.5′N, 76°28.5′W; 55 m; 18 May 1969; USNM 727773.—2 ♂, 1 ♀, 40-45 mm; *Pillsbury* sta. 352; 8°20.1′N, 76°53.6′W; 55-51 m; 11 July 1966; Univ.

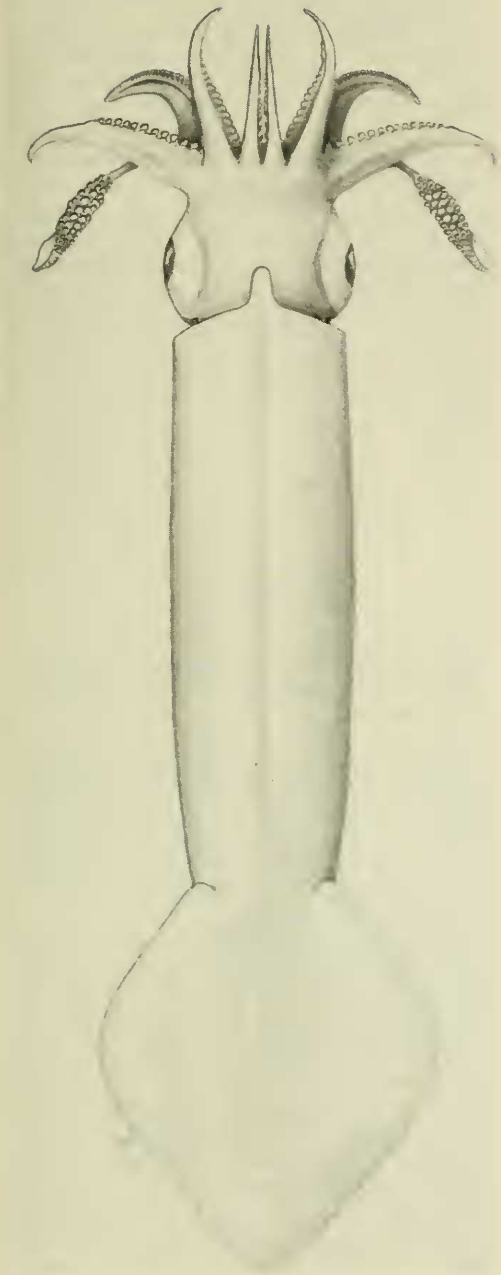

FIG. 27. *Loligo roperi* Cohen, n. sp.; holotype, ♂, 70.8 mm ML; *Geronimo* sta. no. GE-8-26.

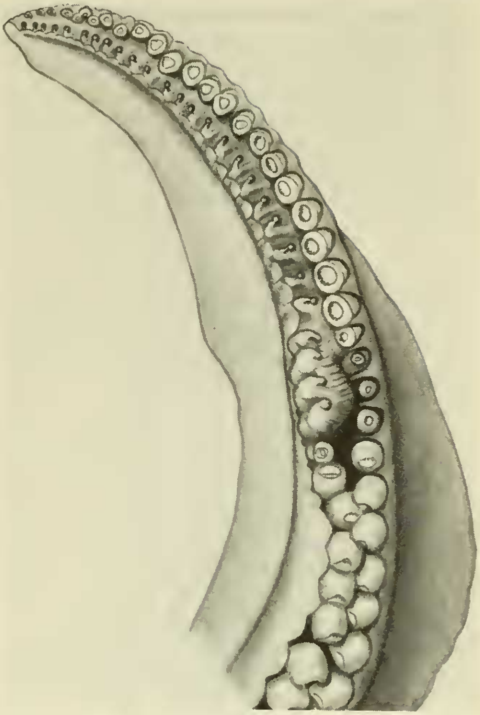

FIG. 28. *Loligo roperi* Cohen, n. sp.; hectocotylus; holotype, ♂, 70.8 mm ML; *Geronimo* sta. no. GE-8-26; entire arm (arm length 14.8 mm).

Miami. Other material: 26 ♀, 44-50 mm ML; *Oregon II* sta. 187; 14°49′N, 81°39′W; 48 m; 19 Nov. 1968; USNM 727772.—1 ♀, 44 mm; *Oregon II* sta. 223; 9°37′N, 76°1′W; 55 m; 28 Nov. 1968; USNM 727771.—1 ♀, 46 mm ML; *Silver Bay* sta. 2477; 25°13′N, 79°13′W; 366 m; 8 Nov. 1960; USNM 575884.—1 ♂, 53 mm ML; off Woodbridge Bay, Dominica, B.W.I.; night light; 13 Nov. 1964; USNM 575874.—3 ♀, 40-43 mm ML; 8°49.2′N, 77°21.2′W; dip net; 17 July 1966; Univ. Miami.

DIAGNOSIS: small (none observed larger than 72 mm in ML), mature at small size (mature males of 44 mm ML, mature females of 43 mm ML); tentacular clubs with not more than 25 transverse rows of suckers in 4 longitudinal series containing not more than 105 suckers total; hectocotylus occupies over 50% of the distal part of the left ventral arm, extends to tip of arm, about 80% (77-89%) of the suckers of the dorsal

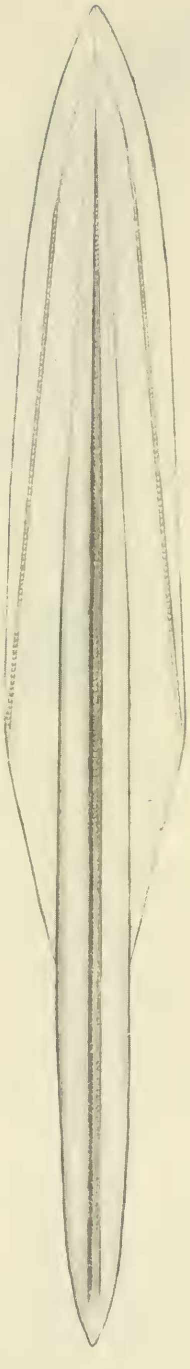

FIG. 29. *Loligo roperi* Cohen, n. sp.; gladius; ♂, gladius length 44 mm, Cohen spec. no. 17; *Oregon II* sta. no. 187.

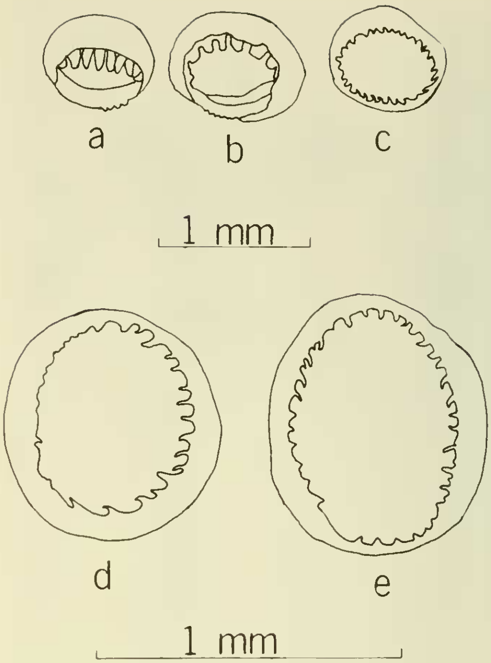

FIG. 30. *Loligo roperi* Cohen, n. sp.; teeth ring of largest sucker on arm III: **a, b** (holotype); teeth rings of large mid-manal sucker of tentacular club: **c, d** (holotype), **e.**

row modified: minute suckers upon broadly triangular pedicels; no suckers on ventral lappets of buccal membrane, not more than about 6 suckers total on buccal membrane, ventral lappets short, often do not extend beyond membrane, 5-7 lappets but 7 buccal connectives and 7 supporting rods.

DESCRIPTION: *Mantle* long, slender, cylindrical, tapers to a posterior acute point (30-35°). Mantle broadest anteriorly in males, broadest near midpoint in mature females (corresponding interiorly to posterior portion of accessory nidamental glands, anterior portion of egg mass); anterior mantle width about 16-26% of ML (40-72 mm ML), greatest mantle width in mature females about 18-27% of ML (40-72 mm ML), longer specimens of both sexes more slender. Ventro-lateral lobes on mantle opening short and pointed (point approximately 90° angle); dorsal lobe longer than lateral lobes, with rounded point; low, narrow ventral ridge present on males.

Fins rhomboid, curved lateral and anterior margins give a somewhat heart-shaped or oval appearance to fins of some specimens (mostly females); widest point curved and anterior to or at midpoint of fin length; fins united posterior to tip of mantle; length (33-39% of ML, 40-72 mm ML) about equal to or slightly less than width (31-50% of ML, 40-72 mm ML), fins relatively large in short specimens, ratio of length to width = 0.7-1.17 (40-72 mm ML); anterior lobes well-developed.

Funnel well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheet-like. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute and bluntly pointed at tip. Ventral pads oblong, shorter than dorsal pad. Funnel valve broad, blunt, with thin curved lateral flaps.

Funnel locking-cartilage long (about 13-16% of ML, 40-72 mm ML), straight, posterior end slightly wider and curved dorsally, shallowly grooved. Mantle locking-cartilage straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head width about 19-27% of ML; length about 12-25% of ML (40-72 mm ML), head relatively small in large specimens; nuchal cartilage long (about 15-19% of ML, 40-72 mm ML), straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to rounded and blunted points respectively; shallow central groove, lateral ridges distinct. Eyes oval, covered by cornea, pupil round. Diameter of externally visible eyeball about 11-16% of ML, diameter of dissected lens about 3-6% of ML (40-72 mm ML), eye relatively small in large specimens. Dark, sometimes greenish crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order III⩾IV⩾II>I or III⩾II⩾IV>I; length of arm I about 14-27% of ML; length of arm II about 18-34% of ML; length of arm III about 20-38% of ML; length of arm IV about 18-36% of ML (43-72 mm ML). Arm III robust, arms II, IV less robust, arm I least robust. Swimming keels well-developed on arm I, flaring before midpoint, decreasing to very low distally; very low, weak on arm II, decrease distally; best-developed on arm III, flare before midpoint, decrease gradually distally; well-developed on arm IV, 2 keels, decrease gradually distally, dorsal keel better developed, dorsal keel of arm IV and keel of arm III arise from same area of base of arms. Protective membranes well-developed, particularly ventral membranes on arms I, II, III; ventral membrane on arms II, III broadest adjacent to largest suckers; poorly developed, particularly dorsal membrane on arm IV, trabeculae long, strong, except on arm IV, arise from base of sucker stalks, form high points along membranes. Suckers biserial. About 5 proximal-most suckers of arm I increase slightly in size distally. About 5-9 proximal-most suckers on arms II, III increase in size distally; 10-12 suckers large; succeeding suckers decrease in size, decrease sometimes rapid following 20-24th sucker. 1-2 proximal-most suckers on arm IV often smaller than 2nd or 3rd sucker, succeeding suckers decrease in size distally. About 41-54 suckers on arm I; about 53-62 suckers on arm II; about 56-65 suckers on arm III; about 60-76 suckers on arm IV (43-72 mm ML). Arms I, IV sometimes with about 10 less and more respectively than arms II, III. Width of suckers on arms in order III>II⩾I⩾IV.

Arm sucker dentition variable (Fig. 30). Teeth present on distal 1/2 of tooth ring. Low plate on proximal 1/2 of tooth ring. Arm I with about 5-7 usually blunt or bluntly-rounded, sometimes square teeth; central 2-4 teeth sometimes pointed, narrower, often longest; lateral teeth decrease in size. Arm II with about 7-10 teeth; shape ranges from all teeth blunt to all teeth pointed except lateral-most teeth; central 2-4 teeth usually longer, narrower and more pointed than lateral teeth which decrease in size; arm III with 6-8 teeth, shape varies from all blunt to only lateral teeth blunt, central 2-4 teeth usually longer, narrower and more pointed than lateral teeth which decrease in size; arm IV with 3-5 blunt or pointed teeth on distal 3rd of small tooth ring, low broad plate on proximal 2/3 of tooth ring; teeth equal in size or central teeth longer. Smaller distal tooth rings on all arms with relatively narrow teeth.

More than 1/2 of the left ventral arm *hectocotylized* (about 57-62%, 44-71 mm ML) (Fig. 28). Modification, chiefly in the dorsal sucker row, extends to arm tip. About 2-5 proximal-most suckers in the dorsal row equal in size (1st sucker may be smaller); about 1-7 proximal-most suckers in ventral row equal in size; about 1-7 succeeding suckers in dorsal row decrease in size distally; about 2-10 succeeding suckers in ventral row decrease in size distally; next succeeding suckers in dorsal row minute, on enlarged pedicels, 3-5 pedicels most enlarged, 1-2 adjacent ventral suckers very tiny followed distally by about 3-6 large ventral suckers of either increasing or equal size; all succeeding suckers of both rows decrease in size distally, suckers of dorsal row minute (more distinct than proximal 8 most modified suckers), on triangular pedicels. Hectocotylized arm with about 68-86 suckers, 58-68 suckers distal to origin of hectocotylus (about 77-89% of total suckers on arm, 44-71 mm ML). Central area of arm adjacent to about 3-7 most modified suckers raised as a central ridge connecting bases of dorsal suckers.

Tentacles robust. Clubs expanded, about 14-21% of ML (40-72 mm ML). Clubs with 19-24 transverse tetraserial rows of suckers (40-72 mm ML). Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 1-4 suckers; no carpal knobs. Often only 3 suckers in proximal-most row of manal suckers, distal rows tetraserial, suckers increasing in size, about 8-12 medial suckers on manus greatly enlarged; lateral manal suckers smaller than medial suckers; manus terminates rather abruptly, distal-most 1 or 2 transverse rows of manus decrease in size, ventro-lateral sucker becomes large relative to medial suckers. This pattern of transverse gradation of sucker size with ventro-lateral sucker the largest, medial suckers smaller, dorso-lateral sucker smallest, continues for about 5-10 rows of dactylus. Dactylus distinct, short, slender, suckers tetraserial, minute, decreasing in size distally, distal-most 2 transverse rows often with 3 and 2 suckers. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of tentacular stalk aborally, increases in size on manal region of club, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad heavily supported protective membranes along club, diminish significantly along dactylus particularly on dorsal side. Weak trabeculae between lateral suckers, usually broaden and disappear laterally in the shape of a fan; arise from common base of lateral suckers; ventral ones sometimes stronger, absent on dorsal side of dactylus. Largest suckers on club usually slightly larger than largest suckers on arm III; ratio of width of largest tentacular suckers to width of largest suckers on arm III = 0.8-1.3 (40-70 mm ML).

Club sucker dentition variable (Fig. 30). Sucker rings of carpal area usually with low, broad plate on proximal 1/2 of tooth ring, about 8 weak, usually pointed teeth on distal 1/2 of tooth ring, teeth graded in size, sometimes no teeth on entire ring or only blunt stubs on distal 1/2 of ring. Proximal-most lateral manal suckers often with low, broad plate on inner 3rd to 1/2 of tooth ring, sometimes toothed around entire margin, about 5-15 usually pointed or triangular, sometimes curved blunt or bluntly-rounded teeth; teeth usually spaced, graded in size occasionally with tiny teeth between larger ones, largest teeth on lateral margin. Largest lateral suckers toothed around entire margin, about 14-30 pointed, narrow or triangular, sometimes curved teeth, graded in size; about 5-12 much larger teeth, on lateral margin; teeth on inner margin often minute, teeth usually spaced, sometimes with small teeth between large ones. Large medial manal suckers with about 25-46 usually pointed triangular teeth of varying sizes; teeth sometimes with rounded tips; large teeth separated by spaces and/or 1-4 smaller teeth of varying height, no regular pattern, occasionally with trinary pattern as follows: large tooth followed successively by small, medium, small and large tooth, but each ring exhibiting variety of patterns, distal-most mid-manal suckers with large teeth on disto-ventral margin of tooth ring. Proximal dactylar sucker rings with about 9-20 teeth graded in size, about 4-8 much larger narrower teeth on distal-ventral margin of tooth ring; teeth fragile, minute, merely a ripple or missing from 1/4 to 1/2 of proximal-dorsal margin of tooth ring; teeth narrow or triangular, pointed, sometimes curved, usually spaced, occasionally with small teeth between a few large teeth.

Gladius (Fig. 29) long, slender (width about 11-15% of gladius length, 40-72 mm ML), feather-shaped; anterior tip with weak flexible acute point; rachis stiff; free rachis length about 24-32% of gladius length (about 22-33% of mantle length, 40-72 mm ML); median ridge and slender lateral rods on rachis continue in center of vane, weaken posteriorly, converge and become indistinguishable near posterior tip. Lateral rods of vane and central ribs of vane joined by diagonal striations, central ends of striations anterior to lateral ends. Rods weaker in females than in males. Ratio of greatest width of vane to greatest width of rachis about 1.9-2.6 (40-72 mm ML). Vane tapered at both ends, sides straight, greatest width in males usually near anterior shoulders of vane, vane gradually narrows posterior to that point; greatest width in females nearer center of vane, located along straight sides between shoulders and midpoint; vane in females does not narrow noticeably until posterior tip. Posterior tip of vane pointed and thin.

Buccal lappets 5-7, 7 buccal connectives, 7 supporting muscular rods (rarely lacks 1); ventral pair of lappets ill-defined, united basally or entirely, often absent in mature females and incorporated into ventral buccal pad on inner surface of buccal membrane for receiving spermatophores; rest of buccal membrane with many inner folds, spermatophores deposited around entire inner side of membrane. Other 5 lappets short, do not project much beyond buccal membrane. Suckers few, 0-3 on each lappet, not more than a total of about 6 on all lappets; suckers usually present on ventro-lateral lappets, rare on 3 dorsal lappets, apparently never present on ventral pair. Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I-IV respectively (specimens examined 40-72 mm ML).

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella) heavily pigmented, notch often separates rostrum and rostral lamella (jaw angle acute or recessed); cutting edge of rostral lamella straight or curved; palatine lamella weak, large, long, deep, slightly pigmented, dorsal crest shallowly curved, slight indentation in lateral wall. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge straight or slightly jagged, jaw angle obtuse, nearly 90°; rostral lamella nearly straight, narrow, short, wing lobate, thin; gular lamellae large, weak, not ridged, posterior corner pointed or with curved point; hood and rostrum short in comparison with wing length and gular lamella length.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth and pointed lateral cusp; 1st lateral tooth pointed, sometimes narrow, with pointed lateral cusp; 2nd lateral tooth pointed, longer than 1st, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 68-75% of total length, cement body about 13% of total length, total length about 3 mm in specimens (44-53 mm ML). Oral connection of cement body funnel-shaped.

Gill length about 21-31% of ML. Number of filaments on one side of gill 41-50 (40-72 mm ML).

Color (in alcohol). Reddish-brown chromatophores present on entire mantle, larger and more closely-spaced on posterior half of dorsal side; few ventrally; present only on dorsal side of fins, more widely-spaced laterally; cover entire head, more closely-spaced dorsally, particularly proximal to eyes; few and only on exposed part of funnel and collar; on outer side of arms and tentacles, form longitudinal line on arms IV, sometimes III. Dark, sometimes greenish crescent over dorsal border of eye. Reddish-brown mid-dorsal longitudinal indentation varying in length, sometimes extends posteriorly almost to fins.

HOLOTYPE: United States National Musuem (727777). Paratypes: United States National Museum (727773, 727774, 727775, 727776); University of Miami.

TYPE LOCALITY: 25°42.5′N, 79°20′W off Bimini Id., Bahama Ids.; *GERONIMO* station 8-26, 6 June 1966, night light.

DISTRIBUTION: Continental shelf of Caribbean: off Nicaragua and Colombia; Antilles; Dominica; Bahama Ids.: Bimini and Old Bahama Channel between Cuba and Great Bahama Bank. Taken by dip net at the surface at night; in bottom trawls at depths of 48-304 m.

ETYMOLOGY: This species is named for Dr. Clyde F. E. Roper, curator in the mollusk division at the Smithsonian Institution and to whom the author is deeply indebted for guidance during preparation of her master's thesis and this publication.

DISCUSSION: *Loligo roperi* has been caught in bottom trawls with *L. pealei* and *L. plei*, with *L. pealei* alone, and with *L. ocula* (Table 3).

Some sexual dimorphism occurs in the width and shape of the vane of the gladius, in the width of the mantle, in the shape of the fins, and in a mid-ventral ridge. The margin of the vane is straighter in males, more tapered in females. The width of the vane is 12-15% of ML in females, 11-14% in males. The point of greatest width of the mantle often lies between the anterior opening and the fin insertion in females; in males

TABLE 10. Comparison of western North Atlantic *Loligo* species. The mantle length examined is given in parentheses in mm.

Character	Species			
	ocula	*pealei*	*plei*	*roperi*
Gladius:				
GW:RW	♀ 2.4-2.9 ♂ 2.5-2.7 (80-127 for all characters)	♀2.7-3.7 (87-188) ♂ 2.4-2.9 (55-244)	1.5-2.4 (38-348)	♀ 2.1-2.6 ♂ 1.9-2.3 (40-72 for all characters)
GW:ML	13-17%	10-20% (28-314)	7-22% (40-319)	11-15%
RL:ML	28-35%	7-33% (23-224)	18-33% (40-280)	22-33%
vane edge (outline)	curved	curved; ♂ sometimes straight	straight; ♀ often curved	straight
vane edge (thickness)	thin	thin; rarely ribbed	ribbed; sometimes weakly	ribbed
Hectocotylus:				
modification extends to tip?	no (some slightly reduced)	no (some slightly reduced)	yes	yes
origin of hectocotylus to arm tip—% of arm length	25-33%	25-33%	26-50%	57-62%
origin of hectocotylus to arm tip—% of total arm suckers	54-62%	47-69%	52-69%	77-89%
Tentacle club: no. of transverse rows of suckers	32-39	30-45 (20-315)	27-38 (31-348)	19-24 (40-72)
TCL:ML	24-35%	20-38% (60-315)	19-29% (44-348)	14-21%
Eye:				
ED:ML	15-21%	8-18% (25-237)	14-19% (40-319)	11-16%
LD:ML	6-8%	2-6% (72-291)	2-7% (40-348)	3-6%
Fins:				
FL:ML	43-54%	44-64% (45-314)	35-58% (40-348)	33-39%
FL < ½ ML		less than 55 mm ML	less than 95 mm ML (many in range 95-192 mm ML)	all
FW:ML	45-59%	34-56% (45-315)	33-45% (40-348)	31-45%
FCL:ML	16-17%	10-18% (60-314)	7-18% (60-348)	13-16%
HW:ML	24-34%	12-32% (25-314)	10-41% (40-348)	19-27%
HL:ML	19-28%	9.5-30% (70-315)	10-22% (44-348)	12-25%
AMC:ML	67-89%	39-78% (60-315)	35-68% (44-348)	
AMW:ML	22-29%	14-33% (45-315)	11-25% (49-348)	16-27%
Buccal lappets: total suckers	45-64	35-113	16-66	0-6
suckers on ventral lappets	yes	yes	yes	never
Gills:				
GL:ML	26-35%	23-34%	20-32%	21-31%
no. of filaments	53-127	55-91 (55-315)	53-84 (44-348)	41-50

TABLE 10. Cont.

Character	Species *ocula*	*pealei*	*plei*	*roperi*
Arms:				
ALI:ML	20-34%	19-50%	16-26%	14-27%
ALII:ML	29-42%	22-50%	23-31%	18-34%
ALIII:ML	35-42%	26-45%	25-37%	20-38%
ALIV:ML	31-40%	22-38% (60-315)	21-32% (44-348)	18-36%
No. of suckers:				
AI	90-110	60-125	50-120	41-54
AII	90-110	70-125	70-120	53-62
AIII	90-110	70-125	70-120	56-65
AIV	95-120	84-132 (40-315)	90-130 (40-348)	60-76

it is more often at the anterior opening. The fins of most males are more rhombic in shape than those of most females. In males the anterior margin of the fin is usually straight; in females it is more often curved. Males have a mid-ventral ridge on the mantle.

COMPARISON OF SPECIES

IDENTIFICATION: Since *Loligo* is a myopsid squid, the lens of each eye is completely covered by a cornea; this easily differentiates it from superficially similar oegopsid squid which always have an oval opening in the skin around the eyes, exposing the lens to sea water. Table 10 and graphs in Figs. 5-7, 9-11, 19-24 compare the 4 species of *Loligo* found in the western North Atlantic Ocean. The hectocotylus quickly identifies mature male *L. plei* and *L. roperi* and distinguishes them from *L. pealei* and *L. ocula* (Figs. 4, 16, 26, 28). In all 4 species the left ventral arm is modified, but modification extends to the tip of the arm only in *L. plei* and *L. roperi*. Modification (hectocotylization) is defined for these purposes as reduction of dorsal suckers to less than 1/2 the size of the ventral counterparts. In *L. plei* the hectocotylus occupies less than 1/2 of the arm (less than 70% of the dorsal suckers); in *L. roperi* the hectocotylus occupies more than 1/2 (at least 55%) of the arm (more than 75% of the dorsal suckers). *L. roperi* is the smallest and most distinctively different of the 4 species. All sexes and sizes of *L. roperi* above 20 mm ML can be identified by the small number of suckers on the tentacles, arms, and buccal lappets, and by the small number of filaments on the gills (Table 10). The largest *L. roperi* examined (72 mm ML) do not have more than 24 transverse rows (of 4 suckers each) of tentacular suckers, while *L. pealei* and *L. plei*, longer than 20 mm ML, have at least 28 rows of tentacular suckers. *L. roperi* shorter than 40 mm ML were not available and may have even fewer suckers and gill filaments. All *L. ocula* examined were at least 80 mm ML; they have at least 32 rows of tentacular suckers. The tentacular clubs of *L. roperi* are also correspondingly shorter than those of the other species. The buccal lappets of *L. roperi* do not bear more than 6 suckers altogether and the ventral pair bear no suckers at all; the buccal lappets of the other 3 species bear more than 16 suckers, and always bear suckers on the ventral pair.

All sizes and sexes of *Loligo ocula* and *L. pealei* can be distinguished from *L. plei* by comparison of the ratio of greatest gladius width (vane width) to greatest rachis width (Table 10). The width of the vane is at least 2.4 times that of the rachis in *L. ocula* and *L. pealei* but is less than 2.4 times that of the rachis in *L. plei* which has both a relatively narrower vane and a wider rachis. Furthermore because the vanes of mature *L. pealei* and *L. plei* are wider in females than in males, the difference between mature *L. pealei* and *L. plei* in this ratio is greater between members of the same sex. Small immature specimens can be separated by this character. This ratio can be determined either by removing and measuring the gladius or by measuring it in place as follows: make an antero-posterior cut along the mid-ventral line. Then either:

1) gently insert finger under gladius, free-

ing it from its attachment along the mid-dorsal line of the mantle. Remove and measure gladius, or

2) gently insert finger between internal organs and gladius, freeing organs from the gladius which lies dorsal to them. Use dividers to determine the relative vane width:rachis width without removing the gladius.

Loligo ocula most closely resembles *L. pealei*; these 2 species are the most difficult of the 4 to differentiate. They differ most in relative size of eyes; the eyes are noticeably larger in *L. ocula*. Measure the diameters of the externally visible eyeball and of the dissected lens. In *L. ocula* the diameter of the dissected lens is at least 6% of ML; in the other species it is 6% or less. Since growth is allometric, the differences are more apparent on a graph (Figs. 19, 20). The modified suckers in the hectocotylus of *L. ocula* are all based upon broadly triangular pedicels, while those of *L. pealei* are, at least in part, based upon narrow pedicels. In addition *L. ocula* usually has a larger head and a longer free rachis, funnel cartilage, and nuchal cartilage than the other 3 species; these characters however show considerable overlap (Figs. 21, 23, 24).[4]

COMPARISON OF *LOLIGO PEALEI* AND *L. PLEI*: *Loligo pealei* and *L. plei* overlap in all characters examined except the hectocotylus and (with one exception among 580 examined) the ratio of greatest gladius width to greatest rachis width. A comparison of Figs. 3 and 5 shows how similar the 2 species, particularly the females, appear. The hectocotylus of *L. plei* extends to the tip of the arm and in *L. pealei* does not (Figs. 4, 26). However, in many *L. pealei* slight reduction of suckers extends distal to the modified area. In some cases this slight reduction extends to the arm tip. But in *L. pealei* the distal suckers in the dorsal row are always more than 1/2 the size of their ventral counterparts. Table 10 shows that other characters overlap extensively. Since these species of *Loligo* have allometric growth, a better comparison can be made with graphs than indices. The graph plotting fin length against ML shows that fin lengths are similar in all 4 species for specimens shorter than about 65-70 mm ML (Fig. 31). In larger specimens, *L. pealei* and *L. ocula* have the longest fins, *L. plei* shorter fins and *L. roperi* the shortest fins, but there is considerable overlap. The difference increases with increasing ML in *L. pealei* and *L. plei*; above about 170 mm ML there is no overlap between the 2 species, but the regression in *L. plei* is curved upward for the longest specimens, so that in specimens over 300 mm ML, *L. plei* and *L. pealei* apparently have a similar fin length. It is helpful in differentiating the 2 species to note that the fin length is equal to or greater than half the ML in specimens of *L. pealei* longer than 55 mm ML; but in *L. plei* is less than 1/2 the ML in many specimens shorter than 192 mm ML and all specimens shorter than 95 mm ML.

In plots of the lengths of the funnel cartilage, gladius width, anterior mantle width, head width and possibly fin width against ML (Figs. 5, 7, 11, 21, 22), the species show overlapping differences in specimens greater than 65 mm ML: *Loligo ocula* is relatively larger in these characters, *L. pealei* next largest, *L. plei* smaller, and *L. roperi* smallest. The differences become more marked in larger specimens.

LaRoe (1967) also found that *Loligo pealei* and *L. plei* overlapped considerably in most characters. LaRoe listed the most effective characters for separation of *L. pealei* and *L. plei* as the hectocotylus, the relative width of the gladius, and the relative lengths of the fin and funnel cartilage. Adam (1937) stated that the 2 species differ in mantle width and fin length. While these indices show differences, because growth is allometric and values overlap, they are not as useful in separating the 2 species as are the hectocotylus and the ratio of gladius width to rachis width. Compare Figs. 3 and 25.

Voss (1956) and Adam (1937) used the gladius to distinguish between the 2 species. Mature *Loligo pealei* usually possess a gladius with a broad vane and curved borders that are not thickened. *L. plei* usually has a

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[4] Since this paper was submitted, a 5th species of *Loligo* from the western North Atlantic has been described: *Loligo surinamensis* Voss, 1974. This species, which has been found only off Surinam, most closely resembles *L. pealei*. Apparently only the males of *L. pealei* and *L. surinamensis* may be distinguished and by only 2 characters in which they never overlap. The mid-portion of the right ventral arm of male *L. surinamensis* bears sharply pointed teeth; there are apparently never any pointed teeth on the suckers of the right ventral arm of *L. pealei*. In *L. surinamensis* the modified portion of the hectocotylized arm consists of flattened, broadly triangular pedicels forming distinct lappets; in *L. pealei* at least some of the modified pedicels are narrow, rather rounded, not broadly triangular.

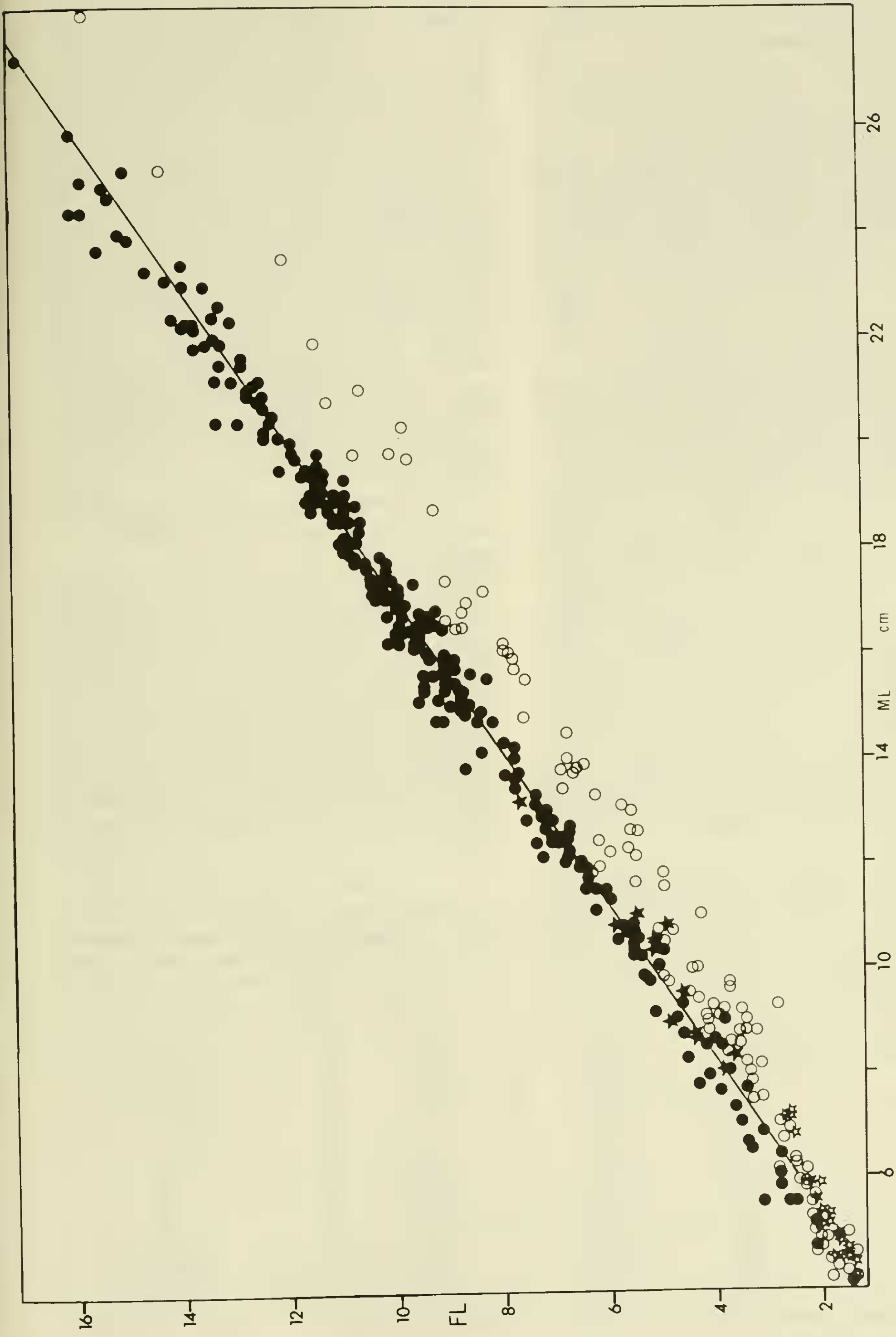

FIG. 31. The regression of fin length upon mantle length (FL:ML). *Loligo pealei* = solid circles and regression line. *L. plei* = open circles. *L. ocula* = solid stars. . *L. roperi* = open stars.

gladius with a narrower blade and straight, thickened borders. However, pigmented but unthickened stripes occur along the margin of many *L. pealei* gladii: 29% of 258 examined have at least a faint stripe; the darkness of the stripe varies considerably. Seven male *L. pealei* of 580 examined have the vane of the gladius with the margin thickened into a lateral rib equal (in some) or almost equal in thickness to any observed in *L. plei*. Some male *L. pealei* have fairly straight edges and small female *L. plei* often have edges that are more curved and scarcely thickened or not at all, in the smallest females. Lateral ribs on the gladius are useful but not reliable by themselves in distinguishing *L. plei* from *L. pealei*.

Voss (1956) and Adam (1937) also use differences in the dentition of the largest tentacular suckers to distinguish between the 2 species. *Loligo pealei* sometimes has a unique trinary pattern of teeth. This pattern has the following sequence: large tooth, small tooth, medium-sized tooth, small tooth, and large tooth. The teeth of the largest tentacular rings of both species often occur in an alternating large and small pattern. Examination of one of the largest tentacular suckers from each of 43 *L. pealei* selected from almost the entire range of distribution showed that the trinary pattern is present in part of the sucker ring of 24, is absent in 15, and doubtful in 4. Of the 15 lacking the pattern, 9 have at least a partial pattern of large-small alternating teeth and 6 have teeth of about equal size. In the 4 doubtful ones the pattern is best described as alternating large and small teeth. The shapes of the teeth are very variable and only the 24 with the trinary pattern are distinct from most *L. plei* teeth patterns. The trinary pattern was also observed in 2 *L. roperi* (20 examined) and 1 *L. plei* (10 examined); it is thus not a useful character.

Ventral ridges occur in males of both species as reported by LaRoe (1967). Of 218 *Loligo pealei* examined, a ventral ridge is at least partially present in 50% and 15% have prominent ridges. Females of *L. pealei* have ridges though they are less prominent. The ventral stripes of chromatophores on the mantle are present on large males of both species, not *L. plei* alone. Ventral stripes occur in 29% of 258 *L. pealei* examined. The darkest stripes occur in the largest males of *L. plei*, but the intensity of the stripes varies considerably. Stripes are not a useful character.

Analyses of covariance were made comparing 13 characters in *Loligo pealei* and *L. plei* (Table 11).

Seven characters show highly significant differences and 6 none. The 2 species are statistically significantly different but overlap in fin length, fin width, head width, gladius width, length of the funnel and nuchal cartilages, and sucker width on arm III (with ML as covariate). There is no significant difference between the 2 species in anterior mantle width, gill length, and number of gill filaments (with ML as covariate), nor with funnel length and length of

TABLE 11. Comparisons of *Loligo pealei* and *L. plei*.

Measurement	Covariate	Adjusted $\bar{X}$ of *L. pealei*		Adjusted $\bar{X}$ of *L. plei*		Significant difference between $\bar{X}$s, p less than
		mm	N	mm	N	
FL	ML	75.3	75	63.4	12	0.001
FCL	ML	18.3	75	16.8	12	0.001
FW	ML	66.3	75	57.8	12	0.001
HW	ML	28.2	75	25.7	12	0.003
NCL	ML	22.9	75	21.2	12	0.006
Fun L	FCL	18.7	75	19.6	12	NS
AL I	FCL	35.2	75	33.4	12	NS
AL III	FCL	46.7	75	47.8	12	NS
TCL	FCL	33.4	75	36.9	12	NS
AMW	ML	30.8	58	25.4	58	NS
F Gill L	ML	33.9	98	31.2	13	NS
F Gill F*	ML	62.3	77	64.0	10	NS
F GW	ML	22.8	22	17.0	22	0.005
M GW	ML	23.9	37	16.9	37	0.005
M ASW III**	ML	2.6	37	1.9	37	0.005

*Variance differences made male results inconclusive.

**F = female, M = male.

arm III (with length of funnel cartilage as covariate). Mantle width was used instead of circumference because this is the measurement used by other workers.

There is no noticeable difference between the spermatophores of the 2 species. Spermatophores of 16 specimens of *Loligo pealei* from 3 locations and 4 specimens of *L. plei* were mounted on slides. Spermatophores taken from 2 specimens of *L. pealei* differ as much from each other as they do from those of *L. plei*. In addition, 16 separate measurements of the spermatophores of 2 *L. pealei* and one *L. plei* were compared and in these also, differences are greater between the 2 specimens of *L. pealei* than between the 2 species. Measurement of additional spermatophores did not seem profitable.

Loligo pealei inhabits waters with a wider temperature range than does *L. plei*. *L. plei* appears not to share the coldest part of the range of *L. pealei*. *L. pealei* does not share the non-continental or most southern parts of *L. plei*'s range.

In the area in which *Loligo plei* is sympatric with *L. pealei*, LaRoe (1967) believed that *L. plei* occurred in slightly shallower depths than *L. pealei*. Although my data are not from a systematic, unbiased year-round sampling of the area, they do suggest that this is incorrect. Off the SE coast of the United States *L. pealei* were caught at 0-154 m and *L. plei* at 0-366 m. In the northern Gulf of Mexico *L. pealei* were caught at 8-393 m and *L. plei* at 0-80 m. In the southern Caribbean *L. pealei* were caught at 0-73 m and *L. plei* were caught at 0-101 m. See Appendix A. They have been caught in the same trawls (Table 3).

In mating behavior no clear differences have yet been observed between *Loligo pealei* (Drew, 1911; Arnold, 1962) and *L. plei* (undersea observations by Waller & Wicklund, 1968). In both species the males compete for females, display color changes while driving off other males, and mate in the same 2 positions. These features have also been observed in some other members of the Loliginidae, as well as some more distantly related squid. More detailed observations have been made of *L. pealei* than of *L. plei*; these include specific patterns of coloration, formation of male breeding hierarchies, and egg mass or egg mass-like objects as a stimulus to mating. The courtship patterns of *Sepioteuthis sepioidea* (a loliginid) are similar but differ in the following ways from those of *L. pealei*: *S. sepioidea* is not stimulated by egg masses and has different courtship color patterns (Arnold, 1965b). Detailed study of *L. plei* may also reveal specific mating behavior.

I have seen no evidence of hybridization or introgression in the morphology of the 264 *Loligo plei* which I examined. However in *L. pealei* I have seen variations in the hectocotylus and even more so in the gladius which show resemblance to the hectocotylus and gladius of *L. plei*. These were described in the discussion of variation in *L. pealei*. The *L. pealei* with gladii very similar to those of *L. plei* were found in areas of sympatry.

The apparently greater variation in Caribbean populations of *Loligo pealei* (described earlier) may be related to sympatry with *L. plei*. The 2 species have been collected in the same trawls and have similar breeding behavior. Neither species shows character displacement, but rather *L. pealei* exhibits suggestions of higher variability and closer resemblance in some characters to *L. plei*. Rare introgression is a possibility but is not established.

Because the 2 species are so similar morphologically, they are here considered congeneric. *Loligo plei* was described as a *Loligo* (Blainville, 1823) and later placed in the new genus *Doryteuthis* by Naef (1912) who did not designate a type-species. Voss (1956, 1960) and later Adam (1937, 1941) and others have followed Naef. LaRoe (1967) placed *plei* in *Loligo* because of its similarity to *L. pealei*. *Doryteuthis* is more similar to *Loligo* than are other genera, but determination as to whether or not it deserves separate generic status awaits study of all of the species of *Doryteuthis*. The affinities of the 4 known western North Atlantic species support the acceptance of *plei* as a *Loligo*. *L. plei* is so close to *L. pealei* that if *plei* is placed in *Doryteuthis*, *L. roperi* must be placed in a new genus. *L. roperi* is the most distinctive of the 4 species.

VARIATION: Some sexual dimorphism occurs in all 4 species. Statistical analysis of variation was made only of samples of *Loligo pealei*, the most variable species. Lateral ribs of the blade of the gladius are stronger in males than in females of *L. roperi* and *L. plei*; they are present only rarely in males, never in females of *L. pealei*, and are not present in the 12 *L. ocula* available to me. The margin of the blade of the gladius is straighter in males, more tapered in females of *L. pealei*, *L. plei*, and *L. roperi*. The blade is noticeably wider in females than in males of *L. pealei* (statistically significant difference) and *L. plei*; it is slightly wider in some females of *L. roperi*; it shows no apparent sexual dimorphism in the 12 *L. ocula*. In mature females the broad portion of the gladius lies above the full ovary and may help support or protect the large mass of eggs in a ripe female.

The presence of eggs is probably the reason that in the region of the mantle posterior to the fin insertion, mature females of *Loligo pealei*, *L. plei*, and *L. roperi* are sometimes wider than males.

In *Loligo pealei* females have about 10 fewer gill filaments than do males (statistically significant difference) of the same ML. Females of *L. ocula*, and *L. roperi* larger than about 65 mm ML, seem also to have fewer gill filaments than do males; there were not enough specimens of either to be certain. Sexes of *L. roperi* smaller than about 65 mm ML and all *L. plei* show no sexual dimorphism in gill filaments. The dimorphism in *L. pealei* suggests that in *L. pealei* the females may have a lower oxygen requirement (as discussed earlier).

A mid-ventral ridge on the mantle is much more common in males than in females of *Loligo plei* and *L. pealei*; it is apparently present only in males of *L. roperi*. Ventral longitudinal reddish-brown chromatophore stripes are present only in some mature males of *L. plei* and *L. pealei*.

Fin shape is slightly dimorphic in *Loligo roperi*: most males have fins which are more rhombic and less curved in outline than those of the females.

Some sexual dimorphism has been reported for other Loliginidae. The males of *Loligo opalescens* Berry, 1911, a closely related species on the Pacific coast of the United States, have longer arms and larger heads than females (Fields, 1965). Fields concludes that these differences are sufficient for visual sexual discrimination by the squid. In the 4 species of *Loligo* considered here, sexual differences in fin width and arm sucker width are not sufficient for visual or field determination of sexes by man. Although statistically significantly different in *L. pealei*, there is a great overlap of values between the 2 sexes even when these are regressed on ML. The differences probably do not contribute to visual sexual differentiation by *L. pealei* or the other species of *Loligo* considered here.

Greater fin width in females than in males was reported also for *Loligo vulgaris* (Férussac & d'Orbigny, 1834-48), which lives along eastern Atlantic shores. In *Alloteuthis africana* Adam, 1950, a loliginid which occurs off the W coast of Africa, females have wider bodies than males. Unlike *L. pealei*, the females of this species have a smaller head and tail than males and the sexes differ in the shape of the ventral arm suckers (Adam, 1952).

As already noted several authors suggest that geographic variation occurs in several characters of *Loligo pealei*; their suggestions are not supported by the results of this study. I found no clines in 50 anatomical measurements made on *L. pealei*. Southern *L. pealei* (Caribbean Sea-Gulf of Mexico) differ in the following ways from northern *L. pealei* (eastern United States Atlantic coast): 1) gill length increases faster in relation to mantle length in the southern squid; 2) there is more variation in the hectocotylus; 3) they apparently mature at a smaller size. Abnormal numbers of buccal lappets occur in *L. plei* collected in Bermuda and in *L. pealei* collected in the Caribbean. As already noted, variation in *L. pealei* appears greatest in areas of sympatry with *L. plei*; much of this variation takes the form of greater resemblance to *L. plei*.

Geographic variation has been reported for several species in the family Loliginidae. Geographic variation in the following characters in *Lolliguncula brevis* was observed: fin length, fin width, sucker size and arrangement, sucker dentition (Voss, 1956); and fin length, fin width, and arm length (LaRoe, 1967). Sasaki (1929) presented weak evidence that *Loligo edulis nagasakensis* and *L. edulis grandipes* are distinct subspecies. Clarke (1962) found some geographic variation in the darkening of beaks of *Loligo vulgaris* Lamarck, 1799, *L. forbesi* Steenstrup, 1856, and *Sepioteuthis lessoniana* Lesson, 1830. I did not find geographic variation in any of the above characters in *L. pealei*.

Several species-specific characters in *Loligo roperi* are characters that vary in *L. pealei*. The number of buccal lappets vary occasionally in *L. pealei* and *L. plei*; in *L. roperi* the lappets are smaller and bear fewer suckers than in the other 3 species. The number of gill filaments are fewer in female than male *L. pealei*; in both sexes of *L. roperi* they are fewer than in the other 3 species. The amount of modification of the hectocotylized arm varies in *L. pealei*; it is greater in *L. roperi* than in the other 3 species.

AFFINITIES: The 4 species of *Loligo* considered here arrange themselves in the following general order of resemblance: *L. ocula, L. pealei, L. plei* and *L. roperi*. This has been noted already in plots of the length of the funnel cartilage, head width, anterior mantle width, gladius width against ML and possibly fin width; and in the fin length and percentage of modification in the hectocotylized arm (*L. pealei* and *L. ocula* are about the same in the last 2 respects) (Figs. 5, 7, 11, 21, 22, 31). *L. ocula* is very similar morphologically to *L. pealei* and differs principally in having larger eyes. *L. ocula* apparently lives in deeper water than *L. pealei*. It is probably closely related to *L. pealei* and may have evolved larger eyes as an adaptation to living in a deeper habitat with less light than that of *L. pealei*. The enlarged head and wider mantle may have evolved in harmony with the eyes—the head to accommodate the larger eyes and the wider mantle opening to accommodate the wider head. The 2 species so far as is now known are allopatric; *L. pealei* strays only extremely rarely from the continental shelf and slope; *L. ocula* usually occurs near islands and in deeper water than *L. pealei. L. pealei* and *L. ocula* may be sympatric on the continental shelf off Honduras; *L. ocula* has been captured there, but *L. pealei* has not. Whether or not they are also separated by any reproductive barriers is not now known. Possibly *L. ocula* is, or its ancestors were, a subspecies of *L. pealei*. I think that the morphological differences are consistent and extensive enough to conclude that they are separate species.

Loligo pealei and *L. plei* differ in more characters than do *L. pealei* and *L. ocula*. *L. roperi* differs from the other 3 in even more characters. It is closer in most characters (length of the funnel cartilage, fin length, head width, anterior mantle width, gladius width) to *L. plei* than to the other species; in the ratio of gladius width to rachis width, *L. roperi* lies between *L. plei* and *L. pealei*.

Loligo roperi is sympatric with all 3 species but apparently has a smaller geographic range than *L. pealei* and *L. plei*. It has been captured in trawls with *L. plei* and *L. ocula*.

Several things suggest that *Loligo roperi* may be an early-maturing (perhaps somewhat neotenic) relative of *L. plei. L. roperi* matures at a small size and apparently does not grow as large as the other species; 72 mm ML is the largest observed. It has much fewer suckers on the arms and tentacles and fewer gill filaments (Fig. 6) than do equally small specimens of the other 3 species; apparently when *L. roperi* reach 40 mm ML (or possibly less) there is no further increase in suckers and little in gill filaments. Furthermore, while the mantle length continues to increase, specimens greater than 50 mm ML (only 12 were examined) show no increase in anterior mantle width, fin width, eye diameter, and lens diameter, and relatively less increase in gladius width and head width than the other species (Figs. 5, 7, 11, 19, 20, 22). In the other 3 species there is continuous increase in all of these characters with increasing ML.

Loligo plei have been found mature at a ML as small as 38 mm and immature at a ML as great as 139 mm. As already discussed, *L. plei* probably do not die immediately after spawning. Catches of *L. plei* sometimes contain small mature specimens with larger immature ones; the small mature specimens can reproduce earlier than the larger immature ones. If there were a genetic basis for early maturity in these specimens, and if it were coupled with death after spawning, there would be a chance for genetic isolation of 2 subspecific groups—early maturers and later maturers. If the early maturers survive spawning and later mate with later maturers, the groups would not be genetically isolated. In comparing small, mature *L. plei* with both small, immature *L. plei* and with large mature and immature *L. plei*, I found no morphological differences which would indicate that separation between early and late spawners is now occurring. I suggest that *L. roperi* could have become separated as a species from *L. plei* or its ancestors in this manner, particularly if ancestors died after spawning. It would be interesting to know how much their niches differ. *L. roperi* probably cannot eat the same food as the larger *L. plei; L. roperi* has a smaller geographic range than *L. plei; L. roperi* may have a narrower niche than *L. plei*.

There are probably 2 ways in which a species of squid can mature at a small size and also attain a relatively large size: 1) survival after a first spawning followed by continuing growth and later spawnings (*Loligo plei* and *L. pealei* may use this strategy); 2) spawning linked to an environmental cue such as temperature change; delay in spawning for some populations until they reach a larger size; death after spawning (*L. pealei* probably uses this strategy, at least in the temperate part of its range; *L. plei* may also use it in the small temperate part of its range). A 3rd strategy is one spawning occurring within a relatively narrow size range followed by death (this is apparently the strategy of *L. roperi*, which lives only in the tropics). This is mere speculation. Studies of the biology of the tropical populations of these *Loligo* have not been made; such studies, as well as observations of live animals, would be useful.

DIVERSITY: Two species of Loliginidae belonging to different genera are also partially sympatric with the 4 species of *Loligo* discussed in this paper. *Lolliguncula brevis* has been caught on the continental shelf and in estuaries from Delaware Bay to Rio de Janeiro, Brazil, and is found in lower salinities than the other loliginids (LaRoe, 1967). It has been caught in the same trawls with *Loligo plei*. In *Lolliguncula brevis* the body is relatively shorter and wider than in *Loligo* and the fins are round or eliptical (not rhomboidal) and wider than long. *Sepioteuthis sepioidea* has been caught in tropical waters from Villegas, Venezuela, to Cape Canaveral, Florida, and in the Bahamas, Bermuda, St. Martins of the Netherlands Antilles, and Cozumel, Mexico (LaRoe, 1967). It has fins which extend the length of the mantle except in tiny newly-hatched specimens (LaRoe, 1967).

All 7 of the western North Atlantic loliginids live in the Caribbean Sea; this sea has the greatest species diversity of the western North Atlantic for not only the genus *Loligo* but the family Loliginidae. Five species: *Loligo pealei, L. plei,* and *L. roperi, Lolliguncula brevis*, and *Sepioteuthis sepioidea* live on the continental shelf off Panama and Colombia. *Loligo plei, L. ocula, L. roperi*, and *Sepioteuthis sepioidea* (and very rarely *L. pealei*) are found off the islands of the Caribbean. *L. surinamensis* Voss is reported off Surinam by Voss (1974). The Gulf of Mexico has only 3 loliginids: *L. pealei, L. plei*, and *Lolliguncula brevis*. Three species live in the Bahamas: *Loligo plei, L. roperi*, and *Sepioteuthis sepioidea* (and very rarely *L. pealei*). Two are found off Bermuda: *L. plei* and *Sepioteuthis sepioidea.* Four species live off the east coast of Florida: *L. plei, L. pealei, Lolliguncula brevis*, and *Sepioteuthis sepioidea. S. sepioidea* is only rarely found farther north. *Loligo plei* is only rarely found north of Cape Hatteras, and *Lolliguncula brevis* is only rarely found north of Delaware Bay, leaving only 1 species—*L. pealei*—off New England and southern Canada.

The Caribbean Sea (in particular the Panama area) thus seems to be the area of greatest species diversity for the Loliginidae and the genus *Loligo* in the western North Atlantic. There is less diversity in the Gulf of Mexico and increasingly less N of Florida, although there is considerable diversity on the E coast of Florida. The greatest diversity is thus in the most tropical, probably most environmentally stable part of the region. In the genus *Loligo*, the 2 apparently more specialized members—*L. roperi* and *L. ocula*—occur only in the tropical North Atlantic; the apparently more variable species—*L. pealei* and *L. plei*—have a wider geographic range extending over a wider environmental range. *L. pealei* seems to be the most variable of these species and it has the greatest geographic range covering the widest range of environmental factors—particularly temperature.

KEY TO THE SPECIES OF *LOLIGO* IN THE WESTERN NORTH ATLANTIC OCEAN[5]

1. Left ventral arm hectocotylized (mature males) 2

   Left ventral arm not hectocotylized 5

2. Hectocotylus extends to tip of arm (diameter of distal suckers of dorsal row less than 1/2 that of their ventral counterparts; Figs. 26, 28) 3

   Hectocotylus does not extend to tip of arm (diameter of distal suckers of dorsal row equal or nearly equal to that of their ventral counterparts) 4

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[5] See Table 10 for more comparative data.

3. Hectocotylus occupies less than half of arm (26-50% of arm length; 52-69% of total number of suckers of arm; Fig. 26); suckers on ventral buccal lappets . . . . *L. plei*

   Hectocotylus occupies more than half of arm (57-62% of arm length; 77-89% of total number of suckers of arm; Fig. 28); no suckers on ventral buccal lappets . . . . . *L. roperi*

4. Eye unusually large (diameter of externally visible eyeball 15-21% of ML, diameter of dissected lens 6-8% of ML (Figs. 19-20); bases of hectocotylized suckers all broadly triangular (Fig. 16) . . . . *L. ocula*

   Eye not unusually large (diameter of externally visible eyeball 8-18% of ML, diameter of dissected lens 2-6% of ML (Figs. 19-20); bases of at least some hectocotylized suckers narrowly triangular (Fig. 4) . . . . *L. pealei*

5. No suckers on ventral buccal lappets; total number of suckers for all buccal lappets fewer than 7; fewer than 25 transverse rows (of 4 suckers each) of suckers on tentacular club . . . . *L. roperi*

   Suckers on ventral buccal lappets; total number of suckers for all buccal lappets more than 15; more than 26 transverse rows of suckers on tentacular club 6

6. Ratio of greatest width of blade of gladius to greatest width of free rachis 1.5-2.4; lateral margin of vane usually thickened and rod-like (fin length less than 1/2 of ML in specimens less than 95 mm ML, often less than 1/2 ML in specimens less than 190 mm ML; Fig. 31) . . . . *L. plei*

   Ratio of greatest width of blade to greatest width of free rachis 2.4-3.7; lateral margin of vane usually thin although often slightly darkened (fin length more than 1/2 of ML in specimens greater than 55 mm ML; Fig. 31) 4

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APPENDIX A. Specimens of *Loligo pealei* and *L. plei* identified for this study.

A. Loligo pealei:

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	Minas Basin, Nova Scotia	–	X, 1970	Petersen	USNM[1]	–
3	Chesapeake Bay, Va.	13	VII, 1968	–	USNM	–
2	off Grand Id., La.	–	VI, 1938	–	USNM	574174
20	28°18′N, 91°26′W	12	I, 1970	–	USNM	–
1	27°48′N, 97°W	155	III, 1917	–	USNM	576938
1	off Rockport, Tex.	–	1951	Baughman	USNM	574693
2	S. of Tortugas, Fla.	102	VII, 1932	64-32	USNM	576929
1	Orient, Long Id., N. Y.	–	VI, 1939	Erdman	USNM	575922
3	Bridgetown, Barbados	0–2	VI, 1969	–	USNM	–
1	30°16′N, 87°15′W	–	–	–	USNM	576921
1	Delaware Bay	–	1881	–	USNM	576928
1	Stonington, Conn.	–	1966	Morrill	USNM	576243
3	Woods Holl, Mass.	–	XI, 1885	Edwards	USNM	577076
2	Beaufort, N.C.	–	1950	Dundee	USNM	574616
2	off Grand Id., La.	–	VI, 1938	38-2	USNM	576926
1	off Cape Ann, Mass.	–	V, 1880	U.S. Fish. Comm.	USNM	576801
6	off Newport, R.I.	–	1880	U.S. Fish. Comm.	USNM	576787
1	Vineyard Sound, Mass.	–	V, 1880	U.S. Fish. Comm.	USNM	576840
1	Vineyard Sound, Mass.	–	V, 1880	U.S. Fish. Comm.	USNM	576841
2	Vineyard Sound, Mass.	–	1875	U.S. Fish. Comm.	USNM	–
1	Vineyard Sound, Mass.	–	V, 1880	U.S. Fish. Comm.	USNM	576839
1	Vineyard Sound, Mass.	–	V, 1880	U.S. Fish. Comm.	USNM	576842
6	Woods Hole, Mass.	–	VI, 1885	–	USNM	50576
2	Vineyard Sound, Mass.	–	VI, 1876	–	USNM	576784
25+	off Beaufort, N.C.	13	V, 1970	*Machapunga*	USNM	–
1	Chandaleur, La.	18	I, 1938	*Pelican*	USNM	574321
1	28°36.5′N, 90°55′W	18	III, 1938	*Pelican*, 33	USNM	574325
1	Woods Holl, Mass.	–	1885	*Albatross*	USNM	50575
47	9°3.5′N, 76°28.5′W	57	V, 1969	*Choco*, 38	USNM	–
16	35°11.5′N, 75°12′W	37	X, 1972	*Delaware II*, 4	NMFS[2]	–
19	34°39′N, 75°39′W	123	X, 1972	*Delaware II*, 9	NMFS	–
46	34°2.5′N, 76°14.5′W	154	X, 1972	*Delaware II*, 20	NMFS	–
2	33°43.5′N, 77°13.5′W	31	X, 1972	*Delaware II*, 24	NMFS	–
10+	38°30′N, 74°53′W	62	VIII, 1967	Va. Inst. Mar. Sci., T165	USNM	–
10+	37°55′N, 74°28′W	58	VIII, 1967	Va. Inst. Mar. Sci., T159	USNM	–
10+	36°36′N, 75°6′W	30	VIII, 1967	Va. Inst. Mar. Sci., T186	USNM	–
10+	36°5′N, 74°52′W	88	VIII, 1967	Va. Inst. Mar. Sci., T189	USNM	–
10+	35°51′N, 75°30′W	22	XII, 1967	Va. Inst. Mar. Sci., T238	USNM	–
12	38°2′N, 74°46′W	29	IX, 1967	Va. Inst. Mar. Sci., T217	USNM	577083
2	36°4′N, 74°45′W	137	V, 1967	Va. Inst. Mar. Sci., 65-1	USNM	577082
4	36°51′N, 74°41′W	88	VIII, 1967	Va. Inst. Mar. Sci., T181	USNM	577075
1	33°48′N, 76°42′W	46	IX, 1959	*Silver Bay*, 1220	USNM	–
2	33°43′N, 76°45′W	55	IX, 1959	*Silver Bay*, 1219	USNM	–
1	30°56.5′N, 80°20′W	37	XII, 1963	*Silver Bay*, 5416	USNM	–

APPENDIX A. Cont.

A. Loligo pealei: cont.

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	33°N, 78°2′W	0	XII, 1960	*Silver Bay*, 2536	USNM	–
1	29°45′N, 80°9′W	0	XI, 1957	*Silver Bay*, 215	USNM	–
1	21°30′N, 92°23′W	158	VI, 1970	*Oregon II*, 11006	USNM	–
1	20°17′N, 92°7′W	72	VI, 1970	*Oregon II*, 11005	USNM	–
13	36°22′N, 74°48′W	110	VII, 1969	*Oregon II*, 10670	USNM	–
2	28°40′N, 91°20′W	26	I, 1970	*Oregon II*, 10888	USNM	–
3	10°7′N, 75°44′W	60	XI, 1968	*Oregon II*, 10214	USNM	–
3	36°11′N, 74°58′W	38	VII, 1969	*Oregon II*, 10675	USNM	–
2	19°10′N, 92°55′W	174	VI, 1970	*Oregon II*, 10995	USNM	–
7	28°18′N, 91°26′W	69	I, 1970	*Oregon II*, 10882	USNM	–
1	28°16′N, 91°26′W	69	I, 1970	*Oregon II*, 10883	USNM	–
1	8°50′N, 76°38′W	46	XI, 1968	*Oregon II*, 10245	USNM	–
4	19°16′N, 92°50′W	274	VI, 1970	*Oregon II*, 10996	USNM	–
1	29°17′N, 88°2′W	194	VIII, 1970	*Oregon II*, 11138	USNM	–
3	10°5′N, 75°40′W	44	XI, 1968	*Oregon II*, 10215	USNM	–
3	28°54′N, 86°26′W	366	II, 1970	*Oregon II*, 10898	USNM	–
3	35°46′N, 74°59′W	55	VII, 1969	*Oregon II*, 10681	USNM	–
10+	36°17′N, 74°52′W	73	VII, 1969	*Oregon II*, 10673	USNM	–
2	35°19′N, 74°59′W	124	VII, 1969	*Oregon II*, 10694	USNM	–
2	35°21′N, 74°58′W	82	VII, 1969	*Oregon II*, 10696	USNM	–
4	35°41′N, 74°54′W	73	VII, 1969	*Oregon II*, 10682	USNM	–
4	29°9′N, 88°15′W	393	VI, 1969	*Oregon II*, 10647	USNM	–
8	8°51′N, 76°51′W	73	XI, 1968	*Oregon II*, 10246	USNM	–
6	9°37′N, 76°1′W	55	XI, 1968	*Oregon II*, 10223	USNM	–
3	28°17′N, 94°58′W	46	VIII, 1966	U.S.F.C., 8	USNM	576320
1	27°36′N, 84°13′W	80	II, 1966	*H. Cortez*, EJ-66-10	FSBC[3]	11597
1	8°49.2′N, 77°21.2′W	0	VII, 1966	*Pillsbury*, 406	UMML[4]	–
10	8°0.1′N, 76°50′W	4	VII, 1966	*Pillsbury*, 357	UMML	–
89	8°20.1′N, 76°53.6′W	53	VII, 1966	*Pillsbury*, 352	UMML	–
1	8°49.2′N, 77°21.2′W	0	VII, 1966	*Pillsbury*, 406	UMML	–
163	8°0.1′N, 76°50.3′W	20	VII, 1966	*Pillsbury*, 357	UMML	–
1	9°51′N, 75°58′W	51	V, 1964	*Oregon*, 4885	UMML	–
3	27°37′N, 96°39′W	46	XI, 1950	*Oregon*, 153	UMML	31.317

Statistical samples are listed in Table 6.

B. Loligo plei:

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	Jekyl Id., Ga.	–	VI, 1932	Lindner	USNM	574857
5	St. John, Virgin Ids.	0	III, 1958	S.I. Bredin Exp.	USNM	576085
4	30°16′N, 87°15′W	–	–	*Grampus*	USNM	576921
4	18°32.15′N, 65°18.45′W	366	II, 1933	Johnson-Smithsonian	USNM	577096
1	Tortugas, Fla.	26	VII, 1932	Schmitt, 56	USNM	576917
2	off Grand Id., La.	–	VIII, 1930	Burkenroad	USNM	574548
18	off Sea Id., Ga.	–	VIII, 1931	Berry	USNM	574327
2	29°40′N, 80°23′W	77	X, 1953	*Gill*, 4-19	USNM	–
20	Great Stirrup Cay, Bahamas	16	I, 1967	Waller, *Deep Diver*	USNM	576456
1	Tortola, Virgin Ids.	0	III, 1958	Schmitt, 4a-58	USNM	576081
7	Gulf of Venezuela	–	1-3, 1971	Ewald, 23	USNM	–
1	Tortola, Virgin Ids.	0	IV, 1956	Schmitt, 115-56	USNM	576241
4	6°38′N, 55°35′W	44	VII, 1957	*Coquette*, 311	USNM	575573
1	Sarasota, Fla.	0	IV, 1949	U.S. Fish Wildlife	USNM	574856
1	Panacea, Fla.	4	IV, 1967	Rudloe	USNM	576911
2	So. Carolina?	–	V, 1966	McCain	USNM	576444
4	off Beaufort, N.C.	0	VIII, 1915	Badger	USNM	574654
2	off Beaufort, N.C.	–	1950	Dundee	USNM	574616
1	30°13′N, 88°26′W	5	VIII, 1967	*George M. Bowers*, 8034	USNM	–
2	30°32′N, 87°14′W	9	–	*George M. Bowers*, 8031	USNM	–
1	30°23′N, 87°15′W	7	VIII, 1967	*George M. Bowers*, 8022	USNM	–
1	30°23′N, 87°15′W	–	VIII, 1967	*George M. Bowers*, 8019	USNM	–
1	St. Davis, Bermuda	–	I, 1931	–	USNM	575199
1	St. Georges Harbor, Bermuda	0	X, 1967	–	USNM	576902
3	St. Georges Harbor, Bermuda	0	X, 1967	*Trident*	USNM	576903
1	Flatts Inlet, Bermuda	–	I, 1968	–	USNM	–
1	Flatts Inlet, Bermuda	–	XI, 1967	–	USNM	–
1	Smiths Parish, Bermuda	–	V, 1969	JB-H	USNM	–

APPENDIX A. Cont.

B. Loligo plei: cont.

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	Harrington Sound	–	VIII, 1969	JB-H	USNM	–
1	Bermuda Biol. Sta., Bermuda	–	V, 1951	Baily	USNM	575766
1	9°3.5′N, 76°28′W	10	V, 1969	*Choco*, 38	USNM	–
15	12°27.7′N, 71°44′W	7	VI, 1969	*Choco*, 50	USNM	–
5	12°N, 72°16′W	5	V, 1969	*Choco*, 11	USNM	–
3	Gulf of Venezuela	–	III, 1971	Ewald	USNM	–
3	32°34′N, 78°46′W	8	VI, 1957	*Combat*, 424	USNM	575408
5	30°8′N, 80°49′W	31	I, 1957	*Combat*, 202	USNM	575446
5	32°34′N, 78°46′W	44	VI, 1957	*Combat*, 424	USNM	575408
1	34°39′N, 75°5′W	366	XI, 1956	*Combat*, c-171	USNM	575441
1	29°N, 80°41′W	18	IV, 1940	*Pelican*, 209-5	USNM	574166
1	28°39.5′N, 91°4.5′W	18	1938	*Pelican*, 81-2	USNM	574320
2	28°39.5′N, 91°4.5′W	18	1938	*Pelican*, 81-2	USNM	574662
8	18°25′N, 67°12′W	–	X, 1966	*Geronimo*, 7-2	USNM	577080
3	off Newport, R.I.	7	VIII, 1880	*Fish Hawk*, 800	USNM	51271
1	off Newport, R.I.	–	1880	–	USNM	33189
1	29°56.5′N, 80°51.5′W	26	V, 1960	*Silver Bay*, 2087	USNM	–
2	17°51′N, 66°8.5′W	37	X, 1959	*Silver Bay*, 2640	USNM	–
1	33°N, 78°40′W	27	X, 1959	*Silver Bay*, 1361	USNM	–
2	34°13.5′N, 76°36.5′W	33	IX, 1959	*Silver Bay*, 1236	USNM	–
1	34°0.5′N, 76°21′W	57	IX, 1959	*Silver Bay*, 1233	USNM	–
1	34°1′N, 77°8′W	27	IX, 1959	*Silver Bay*, 1223	USNM	–
2	33°57.5′N, 77°1.5′W	29	IX, 1959	*Silver Bay*, 1222	USNM	–
4	33°41′N, 77°40′W	0	IX, 1959	*Silver Bay*, 1209	USNM	–
2	34°31′N, 76°51′W	20	IX, 1959	*Silver Bay*, 1259	USNM	–
1	34°40′N, 76°23.5′W	15	IX, 1959	*Silver Bay*, 1251	USNM	–
1	34°21′N, 76°29′W	18	IX, 1959	*Silver Bay*, 1243	USNM	–
3	33°32′N, 77°30.5′W	26	IX, 1959	*Silver Bay*, 1208	USNM	–
1	34°7′N, 77°19′W	24	IX, 1959	*Silver Bay*, 1224	USNM	–
1	29°55′N, 80°38′W	0	VI, 1960	*Silver Bay*, 2139	USNM	–
1	34°24′N, 76°23′W	20	IX, 1959	*Silver Bay*, 1261	USNM	–
2	33°56′N, 77°20′W	27	IX, 1959	*Silver Bay*, 1215	USNM	–
1	34°16′N, 77°34′W	13	IX, 1959	*Silver Bay*, 1226	USNM	–
1	34°55′N, 76°9′W	18	IX, 1959	*Silver Bay*, 1255	USNM	–
1	34°46′N, 76°12.5′W	22	IX, 1959	*Silver Bay*, 1265	USNM	–
1	33°55′N, 77°52.5′W	9	IX, 1959	*Silver Bay*, 1211	USNM	–
1	34°10.7′N, 76°15′W	40	IX, 1959	*Silver Bay*, 1245	USNM	–
1	33°58.5′N, 76°22′W	82	IX, 1959	*Silver Bay*, 1234	USNM	–
2	34°19′N, 77°19.5′W	18	IX, 1959	*Silver Bay*, 1228	USNM	–
1	33°43′N, 76°45′W	55	IX, 1959	*Silver Bay*, 1219	USNM	–
4	8°51′N, 76°51′W	73	XI, 1968	*Oregon II*, 10246	USNM	–
1	20°17′N, 92°7′W	66	VI, 1970	*Oregon II*, 11005	USNM	–
2	8°43′N, 59°10′W	73	IV, 1969	*Oregon II*, 10499	USNM	–
3	8°43′N, 59°10′W	73	IV, 1969	*Oregon II*, 10500	USNM	–
1	29°42′N, 88°40′W	16	V, 1958	*Oregon*, 2193	USNM	575648
10+	19°36′N, 91°47.5′W	44	VIII, 1951	*Oregon*, 425	USNM	575108
2	24°46′N, 82°59′W	46	I, 1951	*Oregon*, 237	USNM	575104
3	30°44′N, 81°12′W	15	I, 1967	*Oregon*, 6324	USNM	–
4	25°24′N, 79°15′W	296	V, 1966	*Oregon*, 6094	USNM	–
5	34°17′N, 77°18′W	20	VI, 1967	*Oregon*, 6761	USNM	–
1	34°13′N, 77°15′W	24	VI, 1967	*Oregon*, 6763	USNM	–
13	29°29′N, 80°11′W	37	XI, 1972	*Delaware II*, 113	NMFS	–
1	34°39′N, 75°39′W	123	X, 1972	*Delaware II*, 9	NMFS	–
2	35°11.5′N, 75°12′W	37	X, 1972	*Delaware II*, 4	NMFS	–
14	33°43.5′N, 77°13.5′W	33	X, 1972	*Delaware II*, 31	NMFS	–
55	34°33.5′N, 75°47′W	91	X, 1972	*Delaware II*, 10	NMFS	–
8	31°24′N, 80°37′W	24	XI, 1972	*Delaware II*, 85	NMFS	–
4	34°13′N, 76°53′W	31	X, 1972	*Delaware II*, 24	NMFS	–
6	31°29′N, 80°7.5′W	38	XI, 1972	*Delaware II*, 80	NMFS	–
1	31°6′N, 80°57′W	18	I, 1967	*Oregon*, 6328	NMFS	–
1	11°39′N, 69°22′W	101	X, 1965	*Oregon*, 5640	NMFS	–
1	32°54′N, 78°38′W	35	I, 1967	*Oregon*, 6376	NMFS	–
2	32°2′N, 80°21′W	18	I, 1967	*Oregon*, 6339	NMFS	–
1	32°55′N, 78°54′W	24	VI, 1967	*Oregon*, 6777	NMFS	–
1	9°35′N, 75°44′W	33	XI, 1968	*Oregon II*, 10226	NMFS	–
10+	Egmont Key, Fla.	9	I, 1966	*H. Cortez*, EJ6634 EJ6630	FSBC	I1742 I1718

APPENDIX A. Cont.

B. Loligo plei: cont.

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	27°36′N, 84°13′W	80	II, 1966	*H. Cortez*, EJ6647	FSBC	11960
19	Tampa Bay, Fla.	6	II, 1966	*H. Cortez*, EJ6666	USNM	–
2	9°30′N, 60°15′W	117	VII, 1968	*Pillsbury*, 699	UMML	–

[1] USNM = U.S. National Museum (National Museum of Natural History), Smithsonian Inst., Washington, D.C.
[2] NMFS = National Marine Fisheries Service, Woods Hole, Mass.
[3] FSBC = Florida State Board of Conservation, St. Petersburg, Fla.
[4] UMML = University of Miami Marine Laboratory.

APPENDIX B. *Loligo* statistics.

Fig. no.	Regression no.	Species	Y	X	Regression	N
5	1	*L. pealei*	♀GW	♀ML	Y=2.0+0.1585Xmm	81
	2	*L. pealei*	♂GW	♂ML	Y=5.2+0.1074Xmm	89
	5	*L. pealei*	GW	ML	Y=3.5+0.135Xmm	70 (120-200 mm ML only)
			Sexes differ (ANCOVA $p < 0.001$)			
	3	*L. plei*	♀GW	♀ML	Y=7.5+0.07364Xmm	12
	4	*L. plei*	♂GW	♂ML	Y=7.1+0.0567Xmm	12
		Species differ (ANCOVA $p < 0.001$)				
6		*L. pealei*	Gill F	ML	Y=48.0+0.134Xmm	173
			Sexes differ (ANCOVA $p < 0.001$)			
7	1	*L. pealei*	♀FW	♀ML	Y=4.5+0.4649Xmm	70
	2	*L. pealei*	♂FW	♂ML	Y=8.6+0.3945Xmm	93
			Sex regressions differ ($p < 0.025$)			
	3	*L. plei*	♀FW	♀ML	Y=–5.2+0.4543Xmm	16
	4	*L. plei*	♂FW	♂ML	Y=22.2+0.2401Xmm	10
		Species differ (ANCOVA $p < 0.001$)				
8	1	*L. pealei*	♀MMW	♀ML	Y=8.6+0.1403Xmm	72
	2	*L. pealei*	♂MMW	♂ML	Y=8.5+0.1293Xmm	79
			Sexes differ (ANCOVA $p < 0.003$)			
9		*L. pealei*	Gill L	ML	Y=8.1+0.204Xmm	208
			Sexes differ (ANCOVA $p < 0.001$)			
10	1	*L. pealei*	♀ASWIII	ML	Y=0.59+0.0102Xmm	81
	2	*L. pealei*	♂ASWIII	ML	Y=0.79+0.0098Xmm	89
	5	*L. pealei*	ASWIII	ML	Y=0.46+0.011Xmm	70 (120-200 mm ML only)
			Sexes differ (ANCOVA $p < 0.007$)			
	3	*L. plei*	♀ASWIII	ML	Y=0.14+0.0109Xmm	8
	4	*L. plei*	♂ASWIII	ML	Y=0.36+0.0094Xmm	12
11		*L. pealei*	AMW	ML	Y=11.6+0.113Xmm	175
		L. pealei	AMW	ML	Y=4.2+0.157Xmm	70 (120-200 mm ML only)
12		*L. pealei*	MMC	ML	Y=30.8+0.365Xmm	218
13	1	*L. pealei*	♀FMW	♀ML	Y=5.3+0.093Xmm	73
	2	*L. pealei*	♂FMW	♂ML	Y=1.5+0.134Xmm	78
14	1	*L. pealei*	♂Gill L	FCL	Y=0.104+2.1Xmm	62 (Eastern Coast U.S.)
	2	*L. pealei*	♂Gill L	FCL	Y=–25.2+3.326Xmm	10 (Gulf Coast U.S.)
	3	*L. pealei*	♂Gill L	FCL	Y=–13.1+2.898Xmm	17 (Caribbean Sea)
21	1	*L. pealei*	FCL	ML	Y=7.4+0.083Xmm	218
	2	*L. plei*	FCL	ML	Y=4.8+0.0814Xmm	20
22	1	*L. pealei*	HW	ML	Y=14.1+0.105Xmm	208
	3	*L. pealei*	HW	ML	Y=9.7+0.133Xmm	70 (120-200 mm ML only)
	2	*L. plei*	HW	ML	Y=10.9+0.0997Xmm	20
23	1	*L. pealei*	NCL	ML	Y=6.2+0.1274Xmm	175
	3	*L. pealei*	NCL	ML	Y=2.4+0.152Xmm	70 (120-200 mm ML only)
	2	*L. plei*	NCL	ML	Y=3.2+0.1282Xmm	20
31	1	*L. pealei*	FL	ML	Y=–15.0+0.6748Xmm	223
	2	*L. plei*	FL	ML	Y=–14.2+0.5572Xmm	38